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# AGGRESSIVE BEHAVIOR

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# Punishment of Irritable Aggression

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In a series of three experiments using a restrained target procedure the influence of shock punishment of shock induced aggression in rats was assessed Regardless of prior experience with shock induced aggression punishment resulted in a suppression of the frequency and total duration of the fighting behavior In addition possible alternative explanations that have clouded studies of punishment of irritable aggression were ruled out by demonstrating that the suppression was not a consequence of altered parameters of shock frequency and duration.

Key words rat punishment shock induced fighting attack latencies

## INTRODUCTION

Moyer (1968) proposed a classification system of aggressive behaviors that postulated 7 distinct kinds of aggression (predatory irritable instrumental maternal inter male sex related fear induced) each with a set of specific eliciting stimuli response patterns and physiological bases Moyer (1973) suggested that the assumptions made about causes of the various kinds of aggression would determine the strategies that might be adopted for aggression control One of the three general tactics that Moyer (1973) indicated might be adopted would be training individual organisms to inhibit aggressive behaviors under aggression evoking conditions A technique often used to train subjects to inhibit responding is that of punishment (Azrin and Holz 1966 Church 1963 Solomon 1964)

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and since 1939 (Dollard et al 1939) punishment has been considered one technique for controlling evoked aggressive behaviors One commonly considered form of evoked aggression is irritable aggression but the use of punishment to control irritable aggression raises some unique problems Since punishment involves the presentation of an aversive stimulus contingent upon a response and since irritable aggression is induced by aversive stimulation the consequence of the punishment of irritable aggression could be additional aggressive behavior

After reviewing the literature on irritable aggression Ulrich Hutchinson and Azrin (1965) concluded that aggression could occur as an elicited reaction to punishment operations Although recent studies have suggested that suppression of irritable aggression could be accomplished using punishment procedures (Azrin 1970 Baenninger and Grossman 1969 Roberts and Blase 1971 Ulrich et al 1969 Wetzel 1972) these data do not unequivocally challenge the Ulrich et al (1965) position Ulrich Dulaney Arnett and Mueller (1973) citing those punishment studies concluded that punishment of irritable aggression could result in decreased frequencies of the punished aggressive response but concomitantly could result in increased aggression directed towards other targets increased duration and vigor of aggression when it occurs or other deleterious side effects In support of that position such concomitants of punishment have occasionally been reported in the form of informal observations (e g Roberts and Blase 1971 Ulrich et al 1969) In addition to informal observations that provide support for the Ulrich et al (1973) position questioning punishment as a technique to control irritable aggression the methodologies of the punishment studies cloud the results and provide no firm basis for challenging the Ulrich et al (1973) position

Shock induced aggression is the major laboratory paradigm for the investigation of irritable aggression in general and punishment of irritable aggression in particular Alterations in either the frequency or the duration of shock presentations can have a profound influence on the occurrence of shock induced aggression (e g Azrin et al 1964 Creer and Powell 1971 Dreyer and Church 1968) Because the punishment of shock induced aggression usually involves the use of shock as the punishment stimulus the punishment procedure necessarily changes the parameters of shock as it impinges on the organism Thus altered shock parameters must be included in systematic controls in order to conclude that punishment procedures influence the evoked aggression To date the punishment of irritable aggression literature does not provide the type of controls necessary to make such a conclusion

## EXPERIMENT 1

If in shock induced aggression in rats attack occurs during the shock interval then shock punishment contingent on that aggressive response would result in

an increase in the shock duration If shock induced attack occurs during the intershock interval then contingent shock punishment would result in an increase in shock frequency Since both more frequent shock presentations and increased shock durations have been shown to reduce the frequency of shock induced aggression in rats it is necessary to determine whether either or both of these conditions would be associated with a punishment operation and to include appropriate control procedures in punishment studies Unfortunately the literature on shock induced aggression does not document the functional relation between shock onset and offset and the occurrence of a discrete attack response The purpose of this experiment was to assess the explicit temporal relation between the occurrence of individual shocks and the occurrence of individual attacks and thereby determine whether response contingent shock punishment would result in systematic changes in shock frequency or duration parameters

Since the results of several studies have suggested that the behavior of individual members of pairs can serve to control the occurrence of shock induced aggression in rats (e g Powell et al 1969 Knutson 1971) the latency to display attack when 2 rats are unrestrained and moving freely about the test chamber is a consequence of the performance of both rats To facilitate analysis and the understanding of the characteristics of attack latency displayed by individual rats a restrained target procedure using a live unanesthetized rat was adopted for use in this and all subsequent experiments

### Method

*Subjects* Thirty 100-day-old experimentally naive male hooded rats from the colony of the Department of Psychology at The University of Iowa served as subjects The animals were housed in 66 X 24 X 17 8 cm community cages with free access to food and water Colony lighting followed a 12 hour light 12 hour dark schedule and all experimental sessions were conducted during the middle of the 12 hour light period

*Apparatus* The 31 8 X 24 X 19 cm fighting chamber was constructed of clear Plexiglas and a grid floor consisting of 4 78 mm diameter stainless steel rods spaced 1 59 cm apart center to center On the lid of the chamber in the corner where the target was restrained a 10 2 X 6 4 X 5 1 cm isosceles trapezoid of 6 35 mm thick Plexiglas was affixed at a 45° angle When the lid was closed this piece of Plexiglas was positioned behind the head of the restrained target rat to prevent the aggressor rat from avoiding shock by climbing on the target At the bottom of the same corner of the chamber was a small door through which the tail of the restrained target could be passed The 2 walls of the chamber immediately adjacent to the target were covered with 0 7 mm thick galvanized sheet metal The electrification of these 2 walls prevented the aggressor rat from avoiding shock by standing on a single grid bar while leaning against a chamber

wall The fighting chamber was positioned in an Industrial Acoustics Company 2.44 X 2.44 X 2.13 m sound attenuating chamber directly adjacent to an observation window Illumination was provided by a 100-watt incandescent lamp located 45 cm above the fighting chamber

The target restraint device shown in Fig 1 consisted of 2 major components a leather harness and a restraint plate similar to that described by Hynan (1976) The leather harness was made from processed cowhide Velcro strips sewn to the harness served as adjustable fasteners to ensure that the harness straps could be tightly secured around the neck and chest of the target rat Sewn to the lateral surface of the harness were two 2.36-mm diameter stainless steel rods



Fig 1 This photograph shows a target held in the restraining device in a manner that closely approximates target restraint in the test chamber For photographic purposes the wa[illegible] and lid were removed and t[illegible] taped panel that is located behind the head of the target during fighting was not inserted

with 6-mm diameter flanges at the end Sewn to the dorsal surface of the neck strap of the harness was a 13-cm long beaded chain These 2 flanged rods and beaded chain helped secure the harnessed rat to the 17.8 X 8.25 cm restraint plate constructed of 1.6-mm thick aluminum Two 3-mm wide slots spaced 4.5 cm apart were milled vertically in the plate and were used to hold the 2 flanged rods A tapered hole for securing the beaded chain was located in the center of the top of the plate A 1 6 cm X 13 cm leather strap covered with Velcro was attached 13 4 cm from the top of the plate This strap was passed across the abdomen of the target rat and secured to the back of the restraint plate At the bottom of the restraint plate was an adjustable tail clamp constructed of Plexiglas and lined with foam rubber to prevent injury to the tail of the target rat This restraining apparatus held the target in a position that closely approximated the stereotyped upright fighting posture and restricted target movements to the head upper torso and forelegs

*Since an unshocked target will be attacked infrequently* (Knutson 1971) *the* target must be shocked on aggression test trials Target shock was generated by a North Hills (Model CS 111) tube-type constant-current dc power supply with a peak output of 300 volts The target shock intensity of 1.5 mA was set using a 22K-ohm resistor across tail electrodes constructed of No 60 alligator clips the ends of which had been smoothed and rounded so that they fit the contour of the tail of the target

Shocks administered to the aggressor rat through the grid floor were generated by a tube type constant-current dc power supply with a maximum output of 150 volts and scrambled by a Gerbrands (Model G5820) carbon brush scrambler The aggressor shock intensity of 2 0 mA was set using a Hewlett Packard 3400A RMS Voltmeter across a 1% precision 150-ohm resistor in series with a current setting resistor of 22K ohms placed across 2 grid bars while the scrambler was in operation The 22K-ohm resistance was chosen as the calibration resistance value because it closely corresponds to the median resistance of rats receiving 2 0 mA shock (Campbell and Teghtsoonian 1958) Both shock sources were not grounded so that the 2 power supplies did not share a common ground so current could not be passed from the aggressor rat to the target rat Shock duration frequency and the intershock interval were programmed by conventional timers and electromechanical circuitry The frequency of aggression and the latency of attack with a resolution of 0 1 second were recorded on electromechanical counters

*Procedure* Five aggressor rats and 5 target rats were randomly assigned to each of 3 groups that were submitted to a single shock-induced aggression test session that used intershock intervals of 3 0 5 0 or 10 0 seconds A target was removed from the community cage and placed in the restraint device and the restraint device was positioned in the fighting chamber over a 5 X 5 cm piece of plastic tape that insulated the scrotum of the target from grid shock. Also, a 3.2

X 4 cm piece of moleskin was placed on each hind foot of the target rat to insulate it from shock. The tail electrodes, coated with EKG Sol electrode paste, were affixed to the tail of the target approximately 2 and 5 cm from the base of the tail. The aggressor rat was then placed in the chamber, and after 10–15 seconds the 2 rats received one hundred 0.5-second duration noncontingent shocks at the intershock interval appropriate to the group membership of the pair. A trained observer recorded instances of attack in response to shock when the aggressor initiated physical contact characterized by biting, boxing, or pawing at the head or forepaws of the target. When the observer depressed the Microswitch that recorded attack, the latency of attack relative to shock onset was recorded.

### Results and Discussion

One pair of animals in the 10.0 second shock interval group was excluded from the latency analysis because of a failure to emit any aggressive behaviors. Although avoidance of shock by aggressor rats was infrequent, the fighting frequency scores were corrected for avoidance and analyses were based on the percentage of shocks received that induced attack. The attack latency scores were categorized as occurring either during the 0.5-second shock or during the intershock interval. Figure 2 presents the mean percentage of shocks inducing fighting for the 3 experimental groups and the mean percentage of attacks initiated during the shock. Although the 3 intershock intervals employed produced different attack frequencies, with the 5.0-second interval producing the highest frequency, the percentage of attacks initiated during the shock were very similar across the 3 groups. Averaged across the groups, 87.5% of all attacks were initiated during the 0.5-second shock. These data indicate that contingent shock punishment of shock-induced aggression in rats would generally result in increased shock duration. Since longer shock durations tend to decrease the frequency of attack (Azrin et al., 1964), the increased shock duration associated with contingent punishment is a possible contributing variable that should be assessed in punishment of shock-induced aggression studies.

## EXPERIMENT 2

The results of Experiment 1 suggests that shock presented contingent on shock-induced attack would result in increased shock duration since the attacks are usually initiated during the shock. Thus, to assess the effects of punishment on shock-induced aggression, the appropriate control group must be exposed to

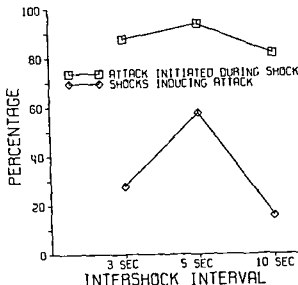



Fig. 2 The mean percentage of shocks inducing fighting and the percentage of shock induced attacks that were initiated during shock by the 3 intershock interval groups of Experiment 1

increased shock duration The present experiment was designed to assess the influence of shock punishment of shock induced aggression relative to the effects of a noncontingent shock duration increase

All the investigations of the punishment of irritable aggression in both primates and rodents have used within-subjects experimental designs That is the animals were first exposed to repeated irritable aggression test sessions to establish a baseline against which the effects of punishment could be compared Thus in all of the reports the subjects had had a previous history of pain induced fighting and were displaying attack at high and relatively stable frequencies when the punishment contingency was introduced A second purpose of this experiment was to determine whether prior shock induced aggression influenced the effects of either punishment or longer duration shock on shock induced attack

**Method**

Subjects One hundred twenty experimentally naive male hooded rats served as subjects The rats had a mean weight of 369 grams and ranged in age from 150 to 173 days old at the beginning of aggression testing For the duration of the study all rats were housed in 66 X 24 X 17 8 cm community cages (6–9 rats per

cage) with free access to food and water On the day prior to the start of the aggression test sessions rats were paired according to weight and housing was re arranged so that aggressor rats and target rats were housed in different cages

Apparatus The aggression test apparatus used in Experiment 1 was used and in addition the frequency latency and duration of attacks were recorded on a computer compatible 8 channel paper tape punch system (Platt and Senkowski 1968)

## Procedure

Phase 1 Aggressor and target rats were randomly assigned to one of the 6 experimental conditions There were 3 treatment groups (punishment increased shock duration and no treatment controls) for each of the 2 fighting history conditions (previous shock induced fighting experience and no shock induced fighting experience) During Phase 1 animals in the 3 previous shock induced fighting experience groups received 5 daily aggression test sessions

Target rats were restrained and positioned in the fighting chamber using the procedure of Experiment 1 During each test session both the aggressor and the target rat received one hundred 0 5 second duration shocks with an intershock interval of 3 0 seconds (onset to onset) In all conditions aggressor rats received 2 0 mA dc foot shocks via the grid floor and the target rats received 1 5 mA dc tail shocks When a target rat received severe lacerations it was replaced with an experimentally naive rat of comparable weight taken at random from an avail able pool of replacement targets Replacement was infrequent and resulted in no apparent effects on fighting behavior Rats in the no previous shock induced fighting experience condition were handled but not exposed to any shock induced fighting test sessions

Phase 2 During Phase 2 the rats from the no prior shock induced fighting group and the group of rats exposed to 5 sessions of shock induced aggression testing were submitted to 1 of 3 manipulations Each aggressor rat of the latter group was paired with a new experimentally naive target for the 5 sessions of Phase 2 During this phase of the experiment all rats were submitted to 5 aggression test sessions consisting of one hundred 0 5 second duration noncon tingent shocks at an intershock interval (onset to onset) of 3 seconds Aggressor shock level was 2 mA dc and the target shock level was 1 5 mA dc This fight inducing shock schedule was the only manipulation used during Phase 2 with the 2 control groups

The aggressor rats in the 2 punishment groups were submitted to additional shocks contingent on attack responses These punishment shocks administered to the aggressor were of the same intensity and duration as the noncontingent foot shocks The target did not receive any punishing shocks because it was in sulated from the grid and shocked from a different power supply During the

Phase 2 sessions when the trained observer depressed the Microswitch when aggression was observed the additional shock was presented to the aggressor Since most attack occurs during shock but the latency of aggression is variable if the delivery of the punishing shock were upon the initiation of attack punished responses would be associated with varying increased shock durations To eliminate this varying duration of the punishment shock these contingent shocks commenced no sooner than immediately after the completion of the noncontingent shock Thus when attack was initiated during the noncontingent shock shock duration was increased from 0 5 to 1 0 seconds Those aggressive responses that did occur in the 2 5 second interval between noncontingent shocks were immediately followed by a 0 5 second duration shock

The aggressor rats of the increased shock duration groups received an additional 0 5 second noncontingent foot shock at the termination of each of the programmed 100 shocks The targets did not receive this shock duration increase and thus received only the 0 5 second duration shocks

During each aggression test session both aggression and avoidance were recorded A maximum of 1 avoidance or 1 aggressive response was recorded for each shock interval in the manner of Experiment 1

In addition to recording the frequency of aggression the latency and the duration of each aggressive response was recorded Upon the observations of attack the trained observer depressed the Microswitch and maintained switch closure until the aggression ceased Response latency was defined as the time between the onset of noncontingent shock and the occurrence of the switch closure Response duration was defined as the time between the switch closure and opening

## Results and Discussion

Although avoidance of shock rarely occurred and was not systematically related to the manipulations the attack data were adjusted for avoidance and all analyses were based upon the percentage of shocks received by the aggressor that induced attack The overall analysis was accomplished using a 3 factor mixed analysis of variance with repeated measures on 1 factor Figure 3 shows the mean percentage of shocks inducing fighting for each group of rats during each treatment session and accurately reflects the statistically significant influence of treatment manipulations ($F = 10\ 06$ $df = 2/42$ $p < 0\ 001$) fighting history ($F = 5\ 32$ $df = 1/42$ $p < 0\ 05$) and sessions ($F = 30\ 04$ $df = 4/168$ $p < 0\ 001$) on the frequency of attack A statistically significant fighting history by sessions interaction ($F = 21\ 51$ $df = 4/168$ $p < 0\ 001$) indicated that the pattern of change in the frequency of attack across the treatment sessions was dependent upon the fighting history of the groups This interaction reflects the fact that the frequency of attack for groups with no fighting history increased as

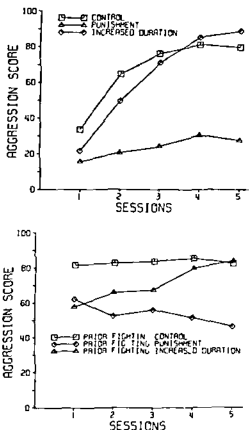



Fig. 3 The mean percentage of shocks inducing fighting for each group during each session of Phase 2 of Experiment 2 The bottom panel shows the Phase 2 aggression of groups that had been tested for shock induced aggression during Phase 1 and the top panel shows the Phase 2 aggression of groups that had no shock induced fighting experience

a function of sessions whereas the groups with a previous fighting history had already reached close to asymptotic levels of fighting at the end of Phase 1 and evidenced less change in frequencies of fighting across the Phase 2 sessions

The statistically significant treatment manipulation by sessions interaction ($F = 7.73$ $df = 8/168$ $p < 0.001$) is shown in Fig 4 which illustrates the mean percentage of shocks inducing attack for the punishment duration and control groups regardless of fighting history at each Phase 2 session An analysis of group differences at each session revealed statistically significant differences at each Phase 2 session (Smallest $F = 3.98$ $df = 2/42$ $p < 0.05$) These simple effects were further analyzed using the Tukey HSD test (Kirk 1968) The duration and control groups did not differ significantly at any of the 5 treatment sessions

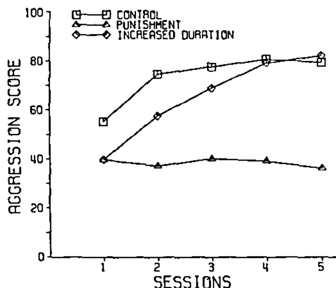



Fig. 4 The mean percentage of shocks inducing fighting at each session during Phase 2 in the 3 treatment condition groups regardless of prior exposure to shock induced aggression testing.

However the frequency of attack for the punishment group was less than the control group at all 5 treatment sessions (Session 1 $p < 0.05$ Sessions 2 3 4 and 5 $p < 0.01$) and less than the duration group at Sessions 3 ($p < 0.05$) 4 and 5 ($p < 0.01$)

To further examine the effects of punishment on the frequency of shock induced attack 2 a priori comparisons were made in a within subjects analysis Using data from the 3 groups with the previous fighting history Session 5 of Phase 1 was contrasted with Session 1 of Phase 2 to assess the initial effects of the treatment manipulation and with Session 5 of Phase 2 to assess the extended effects of the manipulations Both analyses were accomplished using a 2 factor mixed analysis of variance The analyses indicated that the initial effects were not significant but there was a statistically significant interaction for the extended effects of the treatment manipulation ($F = 8.40$ $df = 2/21$ $p < 0.002$) That is the change in fighting frequency from Phase 1 Session 5 to Phase 2 Session 5 was different for the 3 treatment groups Follow up analyses using the Tukey HSD (Kirk 1968) indicated that at Phase 2 Session 5 the Punishment Group displayed a lower fighting frequency than at Phase 1 Session 5 ($p < 0.05$) The increased duration group displayed a higher fighting frequency at Phase 2 Session 5 than at Phase 1 Session 5 ($p < 0.05$) The control group did not change from Phase 1 Session 5 to Phase 2 Session 5 Thus in rats with a history of shock-induced fighting the extended effect of contingent shock punishment

a decrease in shock induced fighting while the extended effect of the increased shock duration was an increase in shock induced fighting

An analysis of variance conducted on the mean duration of attack displayed by each subject during all Phase 2 sessions indicated that both fighting history and treatment manipulations significantly affected the mean duration of attack ($F = 13\ 72$ $df = 1/42$ $p < 0\ 001$ and $F = 11\ 96$ $df = 2/42$ $p < 0\ 001$ respectively) Follow up analyses using the Tukey HSD (Kirk 1968) indicated that the mean duration of attack of punishment and duration groups did not differ significantly (0 77 and 0 82 second respectively) but those mean durations were significantly ($p < 0\ 01$) greater than the mean duration of aggression of the controls (0 60 second)

Since response contingent punishment resulted in an increase in the mean duration of attacks the question of the effects of punishment on the total duration of aggression was systematically examined A 2 factor completely randomized analysis of variance indicated that both fighting history and punishment influenced the total duration of aggression ($F = 11\ 89$ $df = 1/28$ $p < 0\ 005$ and $F = 4\ 55$ $df = 1/28$ $p < 0\ 05$ respectively) The mean total duration of fighting was less for the groups with no shock induced fighting history (138 6 seconds) than it was for the groups with previous shock induced fighting experience (254 1 seconds) Of course this difference merely reflects the different fighting frequencies displayed by these 2 conditions The response-contingent punishment resulted in a lower total duration of aggression in the group with fighting history (234 35 seconds) and the group with no fighting history (86 99 seconds) relative to the 2 comparable control groups (273 98 and 190 29 seconds respectively) Thus while the contingent shocks increased the mean duration of individual attack responses this increase was not comparable to the decreased frequency of attack relative to the control groups and consequently the total duration of fighting was reduced by contingent shock punishment

In order to assess the appropriateness of the increased shock duration comparison group it was necessary to determine the proportion of punished responses that resulted in shock duration increases An analysis of variance indicated that the 2 punishment groups did not differ with respect to the percentage of attacks initiated during shock Thus collapsing across groups 73% of the punished attacks resulted in shock duration increases and 27% resulted in a shock frequency increase Since the punishment shocks resulted predominantly in shock duration increases the noncontingent shock duration increase appears to be the appropriate comparison group However the possibility that the suppression of attack obtained in this study was related to some increases in shock frequency could not be completely excluded with these data

## EXPERIMENT 3

Experiment 2 demonstrated that attack contingent shocks suppressed the frequency of shock induced aggression and that the suppression was not due to an increase in shock duration However the possibility still remains that the obtained suppression may have been partially related to the resulting increases in shock frequency This experiment was designed to determine whether the suppression of attack in the punishment groups of Experiment 2 could have been due to the increase in shock frequency associated with the contingent shocks presented in the intershock interval

### Method

Subjects Fifty experimentally naive 150 day old male hooded rats served as subjects Housing and lighting conditions were identical to those of Experiment 2

Apparatus The apparatus was the same as that used in Experiment 2 with the addition of a paper tape reader to program the delivery of the 100 noncontingent shocks and the randomly distributed additional shocks presented in some intershock intervals

Procedure Aggressor and target rats were randomly assigned to either previous shock induced fighting or no previous shock induced fighting conditions The pairs from the former group were submitted to 5 sessions of shock induced aggression testing following the procedure of Phase 1 Experiment 2 Following these 5 sessions of Phase 1 the targets used in these preliminary sessions were discarded and the subjects of the prior shock induced fighting group were paired according to weight with experimentally naive targets for the 5 experimental sessions During the 5 daily experimental sessions of Phase 2 all subjects received one hundred 0 5 second duration 2 0 mA dc grid shocks with an intershock interval of 3 0 seconds (onset to onset) and simultaneously the targets received 1 5 mA tail shocks following the procedure of Experiment 2 In addition based upon the frequency of contingent shocks presented in the intershock intervals in the punishment conditions of Experiment 2 10 randomly distributed additional 0 5 second duration 2 0 mA grid shocks were presented to the aggressor rats in the intershock intervals

### Results and Discussion

The frequency of attack data were adjusted for avoidance and all analyses were based upon the percentage of shocks received by the subjects that induced attack The control groups from Experiment 2 were used for comparison Figure

5 shows the mean percentage of shocks inducing attack in the 2 groups submitted to noncontingent shock frequency increase and control groups of Experiment 2 A 3 factor mixed analysis of variance with repeated measures on 1 factor indicated that the obvious fighting history by session interaction was statistically significant ($F = 20.46$ $df = 4/112$ $p < 0.001$) Although shock induced fighting experience ($F = 4.20$ $df = 1/28$ $p < 0.05$) and sessions ($F = 18.99$ $df = 4/112$ $p < 0.001$) significantly influenced the frequency of attack the groups submitted to a noncontingent increased shock frequency did not differ from the control groups Thus the increased shock frequency did not significantly alter the frequency of shock induced attack

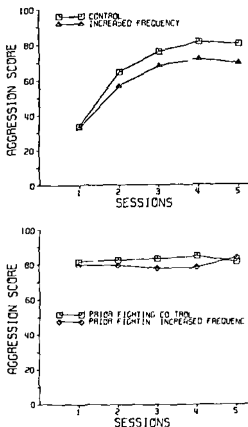



Fig. 5 The mean percentage of shocks inducing fighting during Phase 2 in the 2 control groups of Experiment 2 and the 2 increased shock frequency groups of Experiment 3 The bottom panel shows the performance of groups that had exposure to shock induced aggression testing during Phase 1 and the top panel shows the aggression of groups that had no prior exposure to shock induced aggression

## GENERAL DISCUSSION

The results of these experiments corroborate the findings of Roberts and Blase (1971) that a stimulus of the same intensity and duration used to induce aggression can function to suppress aggressive behavior when that stimulus is presented contingent on the occurrence of that aggressive response The results also indicated that the response-contingent shock punishment functioned to sup press shock induced attack regardless of fighting history This means that within the range of the 5 punishment sessions employed and regardless of whether the animals were attacking at high and stable frequencies or low and unstable fre quencies the shock punishment reduced the subsequent probability that the noncontingent shock would result in attack These experiments also indicated that neither noncontingent shock duration increases nor noncontingent shock frequency increases would function to suppress the attacks Therefore it seems reasonable to conclude that it was the contingent presentation of additional shock that was responsible for the suppression of attack

Consistent with the informal observations of Roberts and Blase (1971) the data of Experiment 2 showed that the punishment groups evidenced a longer duration of fighting per shock than the control groups regardless of fighting history conditions Because the duration group of Experiment 2 also showed this increased duration of attack and because punishment most frequently in creased shock duration the increased duration of attack during punishment appears to be nothing more than a consequence of the increased shock duration during an attack inducing trial Although the punishment groups had a longer mean duration of attack the total duration of fighting was significantly lower than that of the control groups Thus it seems unreasonable to argue that punishment of irritable aggression will decrease the frequency but increase total duration of attack behavior

Ulrich et al (1973) argued that punishment of a behavior in a social setting will elicit aggression Similarly Azrin and Holz (1966) in their review of the punishment literature argued that the use of punishment is inappropriate in some situations because it will induce aggression These authors based their arguments on the presumed reflexive nature of aggression as a response to aver sive stimulation The data of the present experiments together with the data of Roberts and Blase (1971) suggest that the position held by Ulrich et al (1965) and Azrin and Holz (1966) is not tenable The present findings indicate that the punishment of shock induced aggression can reduce the subsequent probability of shock induced attack and the data are consistent with demonstrations that punishment of other kinds of aggression such as inter male and predatory will result in a reduced frequency of the aggressive behavior (Melvin and Ervey 1973 Myer 1966 Myer and Baenninger 1966)

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# Activity of Creatine Kinase in Mice Under Various "Stress" Conditions

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"Stress induced by swimming immobilization and fighting in male albino mice results in a significant increase of creatine kinase (CK) activity in blood obtained by decapitation. The increase partially depends on motor activity as shown in fighting animals. Males show higher CK values than females. Isolation and even immobilization also lead to higher CK activity the latter to a similar extent as swimming and fighting We believe that CK activity is regulated by processes additional to motor activity

Key words aggression creatine kinase grouping isolation mice stress"

## INTRODUCTION

The increase of CK activity in blood serum of patients with endogenous psychosis which was communicated over 10 years ago (Schiavone and Kaldor 1965 Bengzon et al 1966) has been of considerable interest to psychiatric research since that time As functional alterations of the heart muscle can cause a CK increase even when no manifest infarction is present (Ledwich 1973) and as the CK level depends on motor training (Schnohr 1974) the amount of muscle tissue (Garcia 1974), and motor activity in rats (Loegering 1974) dogs (Bolter and Critz 1974a) as well as man (Kuster et al 1966 Critz and Cunningham 1972 Kindermann 1974 Magazanik et al 1974) the CK test is likely to be of little diagnostic value in psychiatry (Harding 1974) The CK activity is intraindividually constant (Meltzer et al 1970) but day-night rhythm and sleep-deprivation induced changes have to be accounted for (Kupfer et al 1970 Meltzer et al 1970

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Foster and Kupfer 1973) and we have no reference measure necessary to appropriately evaluate the CK level of a newly admitted patient

However there is some evidence that a rise of the muscle and not brain isoenzyme in blood serum of psychotic patients is likely to have something to do with the pathomechanism of affective and schizophrenic psychoses regardless of their motor activity (Meltzer et al 1969 Meltzer 1969 Kupfer et al 1970 Meltzer and Moline 1970a Meltzer et al 1971 Gosling et al 1972 Schweid et al 1973 Goode and Meltzer 1976 Meltzer 1976) High blood serum CK has also been found in relatives of psychotic patients (Meltzer 1969 Meltzer and Moline 1970a Meltzer and Moline 1970b Meltzer 1973 Meltzer 1975a Goode and Meltzer 1976) An important contribution to the discussion about the causes of this phenomenon are Meltzer s findings of histologically authenticated lesions of skeletal muscles in psychotics as well as in their relatives (Engel and Meltzer 1970 Fischmann et al 1970 Meltzer and Moline 1970b Meltzer and Engel 1970 Meltzer 1972 Meltzer 1973 Meltzer 1975b) Until now the exact connections between this enzyme and muscle alterations have remained obscure Together with genetic factors social stimuli are frequently claimed to release certain psychoses The importance of stress for the manifestation of endogenous psychiatric diseases is usually accepted yet specific triggers are still not known We also know little about how social stimuli affect somatic processes and how to differentiate them from genetic influences (Elsasser et al 1971 Diebold 1973 van Praag 1975) The concept of stress is rather vague and there are few methods to quantify stress objectively Biochemical methods such as determination of (nor)epinephrine free fatty acids triglycerides cholesterol and protein bound iodine (Levi 1973) and even interferon (Palmblad et al 1974) may be of value But hitherto it has not been possible to identify specific psychosocial stimuli which regularly trigger specific psychic dysfunctions nor can the extent of stress be inferred from the metabolic changes measured (Polzien and Roggenkamper 1972 Brown and Heninger 1975 Selye 1976) The lactate hypothesis[1] of Pitts (1969) has been critically evaluated in the meantime (Grosz and Farmer 1972) and it has been shown on diverse clinical and biochemical findings that high blood lactate levels do not positively correlate with anxiety symptoms (Rahe et al 1972)

At this point it may be mentioned that psychosocial stress will as a rule be followed by enhanced muscular activity including isometric tension The assumption that the CK fluctuation in psychotic patients is not an epiphenomenon merely of motion is supported by several findings It occurs in clinically healthy relatives of psychotic patients and sometimes days before the outbreak of a

[1] Anxiety symptoms were induced in susceptible patients by sodium lactate infusion. Pitts (1969) also claims that as a rise in blood lactate results from exercise that most patients report that physical activity can bring on or intensify their (anxiety) symptoms

psychosis (Meltzer 1968) Yet in the latter condition it has to be taken into account that the patient may already have had a considerable increase in motor activity – at least isometrically – in the time before the overt outbreak of the psychosis On the other hand it has also to be taken into account that isometric tension is unlikely to be a major causative factor in CK rise which is also negligible in the stiff man syndrome (cited from Meltzer and Moline 1970a Goode and Meltzer 1976) or in heavily disturbed neurotic patients (Meltzer 1973) with high muscular activity Furthermore controls of outcome in schizophrenia over a long time have shown fluctuating CK levels partially independent of the course of motor behavior (Van der Velde 1976)

The origin of the elevated CK activities in blood of nonpsychotics under stress or psychotics is largely unknown One possible mechanism is an alteration of the muscle cell membrane (Foster and Kupfer 1973) so that the enzyme can penetrate into the blood In this case it need not necessarily be assumed that CK activity in the muscle itself increases Another cause would be an increase in quantity or activity of muscle CK followed by augmented enzyme activity in serum provided there is a balance between muscle cell and blood

A further exploration of the described enzyme changes by animal experiments seemed to be possible and interesting after one of us (Matte 1975) found an increase of CK in aggressive mice Although there are no animals available in which endogenous psychoses can be identified the influence of motor activity on certain situational stimuli however can be realized experimentally Therefore we studied the effects of isolation different motor activities and immobilization on the activity of CK in the blood of mice

## MATERIALS AND METHODS

This experiment was carried out with 9 week-old inbred albino mice [(Han) NMRI] which were housed grouped or isolated for a further 9 weeks Food and water were given ad libitum They were kept in translucent cages in an experimental room with a constant temperature (21 C) and a window so that diurnal rhythm was maintained The isolated mice served as a control for the following experimental groups which consisted of previously isolated animals One group had to swim for 1 hour We chose a water temperature of 27°C in order to emphasize the effects of anxiety and of motor effort rather than of hypothermia (Stone 1970) Another group of mice was immobilized for 1 hour by taping limbs and trunk to the table with adhesive plaster We gained the impression that these mice submitted fairly easily to immobilization making no attempt to escape In another situation male mice with an isolation syndrome (Valzelli 1973) were mixed in order to fight for 0 5 hour and 1 hour The animals displayed a full range of agonistic behavior such as attack and defense e g biting tail rattling submissiveness arcade forming squeaking and flight reactions With

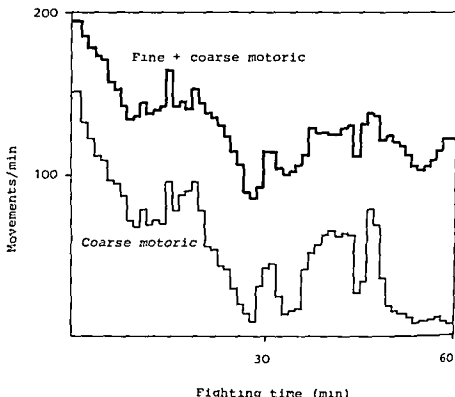



Fig 1 Motor activity of mice during fighting Plotted are sliding mean values of 3 consecutive minutes

increasing fighting time the opponents performed more frequent and longer recreation pauses renewed fighting being initiated by an inciting spark (Fig 1)

Locomotor activity was registered by an Animex DS (Farad AB Sweden) which measures fine and coarse movements by means of magnetic field alteration The coarse motor activity of mice proved to be very suitable as a quantitative parameter of aggressive behavior The confidence limits of the correlation coefficient between measured fighting times and counts of coarse motor activity have been calculated as 0 885 and 0 933 for a 95% probability (Matte 1973)

Decapitation followed directly after test performance with a pair of scissors The outflowing blood was funnelled into a tube and immediately centrifuged (10 minutes 1 500 X g) the serum was then pipetted off and analyzed for CK activity CK was measured with a test set of Boehringer Mannheim which uses the glutathion activated reverse reaction (Szasz et al 1970) The normal value in

venous blood serum of man is 10–30 U/liter with an upper limit of 50 U/liter whereby one unit corresponds to 1 μmol/liter/min (25 C) creatine phosphate converted All sera were diluted 1 5 with isotonic salt solution

## RESULTS AND DISCUSSION

Results are shown in Table I Significant rises of CK were obvious in all stressed groups in comparison with the control group This may indicate that the stress situations used result in an increase of muscle CK activity Thus the increase of serum CK activity often registered in man under heavy physical strain (Meltzer et al 1972) can possibly be attributed to an augmentation of CK activity in muscle Registration of the motor activity of the fighting mice reveals that the movements are most pronounced at the beginning of the fighting The group which struggled for only 0 5 hour exhibited the same pattern as the group fighting for 1 hour during the first 30 minutes Computation of coarse and fine movements (see Fig 1) of group H (see Table I) results in a sum of 6 250 counts in the first and 4 364 in the second half hour This corresponds to the CK values which went up to 3 837 U/liter after half an hour s fight and to 4 605 U/liter after 1 hour i e a smaller augmentation in the later course of fighting

Our results show that the increase of CK is of the same order of magnitude in all stress tests namely 2 5 to 3 fold Surprisingly the immobilized mice had similarly high CK values although they showed no marked muscular activity after they were taped down Isolation itself can obviously not account for this because the animals in the reference group had also been separated for the same time Further there are no weight differences between these males therefore decapitation is likely to have damaged similar amounts of muscle tissue in the animals investigated

On the other hand isolation itself also increases CK activity This increase however is small not comparable with those of the stress conditions used and obviously not explainable by motor hyperactivity

Further it is worth mentioning that there is a significant sex-dependent difference in CK of grouped as well as of isolated mice as shown in the comparison of groups A + C to B + D Table I shows details of weight and CK interrelations

Meltzer rejects stress as the sole cause for a CK increase in serum (Meltzer et al 1972 Meltzer 1973) although he regards situational stimuli as triggers for an increase of enzyme activity in psychotic patients (Meltzer 1968) With reference to his observations there is no doubt that various stress factors lead to a rise of CK blood level (Meltzer 1971) The CK level increases under stress conditions such as hypothermia swimming immobilization etc from 2 to 30 times the baseline level – depending on treatment – with considerable deviation within each experimental group In Meltzer s experiments blood was drawn through

TABLE I CK Activity in Blood Serum of Mice Under Different Stress Experiences

| Symbol | No of animals tested | Sex | Treatment | Weight (grams) | CK (U/liter) |
|---|---|---|---|---|---|
| A | 10 | F | Grouped | 33.7 ± 2.2 | 537 ± 297 |
| B | 9 | M | Grouped | 37.4 ± 2.2 | 953 ± 329 |
| C | 10 | F | Isolated | 31.9 ± 2.6 | 878 ± 312 |
| D | 9 | M | Isolated | 39.7 ± 2.7 | 1 516 ± 726 |
| E | 9 | M | Swimming 1 hour | 41.7 ± 3.5 | 4 254 ± 1 776 |
| F | 9 | M | Immobilization 1 hour | 39.8 ± 3.2 | 4 051 ± 1 670 |
| G | 8 | M | Fight 0.5 hour | 39.6 ± 5.2 | 3 837 ± 1 038 |
| H | 9 | M | Fight 1 hour | 39.2 ± 3.4 | 4 605 ± 1 474 |

Significances (Wilcoxon test)

*Weight* A/C NS B/D NS A+B/C+D NS A+C/B+D $p < 0.001$

CK A/B $p < 0.02$ A/C $p < 0.0$[illegible] A+B/C+D $p < 0.02$ A+C/B+D $p < 0.005$ B/D NS B/E till B/H $p < 0.001$
C/D $p < 0.04$ D/E $p < 0.001$ D/F $p < 0.001$ D/G $p < 0.002$ D/H $p < 0.02$ E/H NS

$r_{\text{body weight/CK activity}}$ (all males) = 0.24 (NS)

puncture of the inferior vena cava under intraperitoneal anaesthesia with a CK activity of 61 U/liter in controls This value is 2–3 times higher than in man This could be due to an efflux of muscular CK into the blood stream caused by the severing of several muscles which is unavoidable with this method Similar CK levels have also been found in the blood of rats and mice (Blumohr et al 1974 Bolter and Critz 1974b Loegering 1974) after heart puncture

The CK content of blood taken immediately after decapitation is largely represented by the muscle enzyme which emerges from the cut muscles and is rinsed into the collecting tube by the streaming blood We believe with Meltzer (Meltzer and Guschwan 1971) that CK values found with this method are about 60 times higher than those from venous blood drawn directly from the vessel The data reported in the aforementioned paper (Matte 1975) are un doubtedly too low because the sera had been stored over a considerable time before being analyzed and therefore a considerable loss of activity must be taken into account This was irrevelant for this particular study as all sera were stored for the same length of time and the study was concerned with establishing relative rather than absolute values The following CK activities (U/liter) which may be based on a formerly used method yielding 50–100 times lower values than determinations with the activated enzyme were found per gram fresh weight in muscle 31 (heart) 155–171 (different skeletal muscles) in man (Dawson and Fine 1967) 217 (heart) and 1 764 (skeletal muscle) in rats (Nuttall 1968) and 117 (skeletal muscle) in mice (Harm 1968)

Some tentative conclusions from our experiments are 'Stress produces an increase of CK in muscle With our method of blood collection (decapitation) the CK is largely of muscular origin It is conceivable that the increase of enzyme activity in blood drawn by venous puncture under avoidance of muscle injury results from adjustment of a balance between cellular and extracellular CK Our results do not speak in favor of a primary alteration of muscle membrane The mechanism of the rise of CK activity in the muscle tissue remains obscure It is unlikely that it is a matter of cortisol induced de novo synthesis as with several other enzymes because adrenalectomy does not hinder the increase of serum CK activity in rats (Meltzer 1971)

One explanation for the sex-dependent difference could be the significant weight differences between the 2 groups which however cannot account for the increase of CK under stress conditions Our findings indicate that CK activity may have some utility as an indicator of the amount of fighting in rodent studies This parameter depends on physical activity but there also seem to be influences on the CK activity independent of motor activity as shown by its elevation under immobilization and isolation

The rise of the CK activity under isolation is a new component in the com plex and disputed isolation syndrome (e g Valzelli 1973 Brain 1975) Doubts have been expressed whether isolation per se can be interpreted as a

stressor (Brain 1975 Goldsmith et al 1976 1977) If CK activity can be used as a measure of stress isolation is a low stress condition

We believe that CK activity is regulated by processes additional to mere changes in motor activity

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AGGRESSIVE BEHAVIOR
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# Aggressive Behaviors of the Japanese Brown Bear

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Film analysis and direct observation suggest that 2 very different types of intraspecific fights occur among Japanese brown bears maintained in large stable colonies. Disputes arising over food are short and involve such activities as threatening muzzling chasing and flight Weapon use during feeding fights primarily involves slashing blows to the back or head areas of the opponent In contrast "spontaneous" fights are longer and consist almost exclusively of wrestling with bites and forepaw blows directed at the opponent s ruff area These spontaneous fights occur primarily among the larger and higher ranked male bears, especially among animals with closely adjacent rankings. It is suggested that such fights facilitate the establishment of dominance relationships by providing an opportunity for mutual assessment of strength and stamina without serious risk of injury

Key words fighting aggression dominance brown bear ursus arctos yesoensis

## INTRODUCTION

Despite the solitary habits of brown bears and the rugged terrain in which they are normally found a number of recent studies have attempted to observe and analyze conspecific interactions in this species Stonorov and Stokes (1972) have reported that Alaska brown bears congregating at the McNeil River falls to

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fish show a clear hierarchy of dominance which is related to specific acts observed during intraspecific encounters The Craigheads (1972) have also made extensive observations of intraspecific encounters among grizzly bears especially at dump or landfill areas where food is concentrated

However for a more precise analysis of specific attack and defensive behaviors in intraspecific bear fights captive populations provide a much higher rate of interaction and certainly better viewing conditions Thus Henry and Herrero (1974) have described in considerable detail the behaviors of young black bears in a zoo setting and Masatomi (1964) has described food dominance and other social relationships among captive Japanese brown bears

The Japanese brown bear (Ursus arctos yesoensis) is a subspecies of Ursus arctos found in relatively dense concentrations in Hokkaido and in the Kurile Island group These animals subsist on a varied diet of vegetable and animal matter including domestic sheep and cattle a factor which has encouraged hunting of the bears Cubs found with killed females are often reared with other captive cubs in one of the several large bear parks found in Hokkaido As they mature these animals are placed in successively larger enclosures with other bears of similar age to form stable though very densely populated groups Although the bears are obviously maintained under conditions quite different than those in which the species has evolved the stability of these groups and the large numbers of like aged animals involved provide an excellent opportunity for extensive observation of intraspecific fighting in the brown bear

## METHOD AND PROCEDURE

### Subjects

The subjects were 37 Japanese brown bears in the Yokuso Bear Park at Teizankei Hot Springs in Hokkaido Japan These bears are maintained in 2 groups with 20 older bears (3 years and older) in a large enclosure and 17 bears under 3 years of age in a smaller pit Both groups were of mixed sexes and most of the animals had been captured as cubs and reared in the bear park The 2 groups were maintained in cinderblock and concrete enclosures one of which was approximately 600 square meters in area (older bears) while the other was about 350 square meters Each pit contained a pool of water deep enough for the bears to partially submerge Food was given twice per day at about 8 a.m and 4 p m but visitors to the park provided a substantial portion of the bears food supply in the form of bread

### Procedure

All observations were made during a 16-day period in late July and early August Two observers spent up to 10 hours per day watching the 2 pits from an

elevated walk atop the wall separating the 2 enclosures and in filming examples of agonistic behavior During an initial period of several days efforts were made to identify and describe each bear in each pit and to determine relative dominance of individual animals Thereafter spontaneous agonistic events and agonistic encounters occasioned by food thrown into the pits were described in terms of the specific participants as well as the behaviors seen Whenever possible films were made of these fights

These films were later analyzed in terms of specific acts displayed by each animal in an encounter for both spontaneous and elicited fights The film analyst had not been one of the observers and the film analysis is therefore relatively independent of the dominance rankings for colony animals which was based largely on feeding fights seen during the initial period of observation

The behavior categories measured during this film analysis included the following approach (moving toward a conspecific) chase (moving rapidly after a retreating conspecific) withdraw (turning or backing away) flight (rapid motion away from a conspecific) standing with orientation (relatively motionless standing with the heads of the 2 animals in close juxtaposition) wrestling (active contact with grasping by forelimbs) lying on the back (lying on the back by an animal which may be pinned by an opponent or with the opponent standing over or nearby) and muzzling or jawing (up and down head motions with open mouth usually such as to bring the 2 muzzles into close juxtaposition) In addition to these categories bites slaps and scratches were noted as were the specific sites on the opponent s bodies to which these actions were applied

Finally during both direct observation and during the film sequences attempts were made to detect and categorize puncture and slash wounds and scars in terms of their exact positions on the bears bodies

## RESULTS

### Agonistic Behaviors During Feeding and Spontaneous Fights

Table I presents separate data on activities during the entire group of filmed fights in the following categories all food fights all spontaneous fights feeding fights for a group of 6 bears which were filmed during both food and spontaneous fights spontaneous fights for this same group of 6 bears These latter categories make possible the direct assessment of differences in the topography of food and spontaneous fights for the same group of participants

The most obvious difference between these 2 types of fights was their duration Food fights were extremely short lasting only a few seconds by far the longest feeding fight seen was a 45 second bout between 2 high ranking animals from the younger colony These specific animals also spent a great deal of time in spontaneous fighting which may possibly have been a factor in the duration of this very long food fight which was more than twice as long as any other food

TABLE 1 The Percent Time and Frequency of Various Brown Bear Behaviors During Spontaneous and Feeding Fights

| Percent Time | All Subjects: Spontaneous Fights (N = 10) | All Subjects: Feeding Fights (N = 23) | Selected Subjects[a]: Spontaneous Fights (N = 6) | Selected Subjects[a]: Feeding Fights (N = 6) |
|---|---|---|---|---|
| Approach | 4 2 | 26 8 | 4 1 | 25 2 |
| Chase | 0 6 | 3 3 | 0 6 | 6 1 |
| Withdraw | 3 0 | 16 1 | 2 9 | 7 3 |
| Flee | 0 6 | 3 3 | 0 6 | 4 1 |
| Stand & Orient | 2 5 | 45 6 | 2 7 | 57 2 |
| Wrestle | 74 2 | 4 6 | 78 2 | 0 0 |
| On the Back | 14 8 | 0 4 | 11 1 | 0 0 |
| Muzzle | 18 3 | 36 6 | 17 7 | 39 8 |
| Mean Frequency Per Minute | | | | |
| Bite | 2 64 | 1 35 | 2 57 | 1 25 |
| Slap | 1 61 | 0 67 | 1 70 | 0 93 |
| Scratch | 0 21 | 2 70 | 0 22 | 1 87 |

[a] Based on 6 animals filmed during both spontaneous and feeding fights

fight observed In contrast the longer spontaneous fights lasted 20 minutes or more On one occasion the 4 largest males of the younger colony participated in a complicated fight in which partners were switched and the fight continued without a pause for over 60 minutes Fighting did not finally end until the arrival of visitors who threw food to the bears Although attempts were made to film the entire sequence for each feeding fight observed at certain periods such fights could not be anticipated and the earliest portions of feeding fights were usually lost the total duration of filmed feeding fights thus slightly underestimates the normal duration of feeding fights For spontaneous fights only selected episodes could be filmed since these fights continued for such long durations Thus the filmed length of spontaneous fights considerably underrepresents the length of such encounters Nevertheless even for the filmed sequences spontaneous fights were reliably longer than feeding fights [$t(31) = 3\ 06$ $p < 0\ 01$] This is in agreement with Masatomi s (1964) report of longer play fights than feeding fights in Japanese brown bears in a similar bear park at Noboribetsu

In this context it might be noted that almost all spontaneous fights occurred entirely or in large part in the pools located in each bear enclosure This location appears to reflect attempts by the animals to dissipate heat engendered by the prolonged and often vigorous activity involved in these fights Thus the ready availability of a body of water may have been an essential factor for the very long durations of some of the spontaneous fights observed

The specific agonistic behaviors seen during these 2 types of fights were also systematically different During the feeding fights 2 types of behavior predominated Nearly 50% of feeding fight times consisted of locomotory behaviors such as approach chase withdraw and flight The other major activity seen was standing with mutual orientation of the 2 combatants while one or both animals threatened The clearest threat behavior seen was a slow sideways motion in which the dominant animal with lowered and slightly twisted head presented its neck and ruff area to the subordinate at the same time the dominant bear was usually reaching for and slowly retrieving the disputed food item Physical contact was rare during these fights and usually consisted of a quick slash or scratching motion of the forepaws made with claws curled slightly forward and raked across the skin surface of the opponent animal

In contrast locomotory approach during spontaneous fights accounted for less than one tenth of fight times while standing and threatening was even less common Instead the predominant activity was wrestling which accounted for about 75% of spontaneous fight durations The category of lying on the back was another index of the importance of wrestling type activities since it usually reflected the results of a wrestling bout with one animal pinned under another or maintaining the pinned posture although the opponent bear had moved out of contact Statistical comparison of these behaviors for animals filmed during

both types of fights showed reliably higher percentages of wrestling during spontaneous fights [T(6) = 0 p < 0 05 Wilcoxin matched pairs signed ranks test (Siegel 1956) used because no wrestling was seen during feeding fights] While reliably more approaches were observed in feeding fights [t(5) = 3 81 p<0 05] standing with orientation also tended to be higher in feeding fights [t(5) = 2 25 0 10 > p > 0 05]

Bites and slaps were very common during spontaneous fights with approximately one bite during each 20 second period However the bites seen were very seldom of a type which produced injury to the bitten animal In fact the most common bites involved seizing a clump of hair on the opponent s shoulder neck area and pulling This tactic in terms of the reactions of the affected animal did appear to cause some discomfort it also sometimes pulled out a considerable amount of hair However it was never seen to produce a visible skin lesion Similarly the frequent slaps seen during spontaneous fights were apparently without major danger to the opponent animal These slaps involve the paw surface with the claws angled backwards Moreover slaps or cuffs were blows directed toward and then rebounding from a surface with no scraping scratching or raking of the claws across that surface

### Target Sites

Figure 1 presents the target sites for bites during spontaneous and feeding fights plus the distribution of bite (punctate type) wounds or scars on bears As this figure indicates the vast majority of bites during spontaneous fights were made at the neck or ruff area of the opponent with only occasional bites at

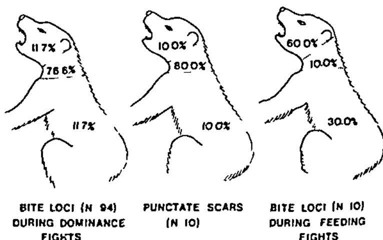



Fig 1 Bite loci during feeding and spontaneous (dominance) fights

head or body areas This finding is in agreement with the observation of Henry and Herrero (1974) that 82% of 'bite and hold reactions of 3 young black bears in a zoo setting were made to the lateral neck and shoulder areas The distribution of bites during the present spontaneous fights was paralleled by the locations of the 10 punctate scars seen on colony bears of these scars 80% were located in the area of the ruff It might be noted that these small punctate scars would probably not have been visible had not the ruffs of several bears been thin possibly due to pulling out of fur during the spontaneous fights

Although only a few bites were seen during feeding fights these bites were very differently distributed on the bodies of the bitten animal 60% were on the head and only 10% in the area of the ruff This pattern is quite similar to that reported by Herrero (1972) of 70% bites to the head in aggressive encounters of black bears at a feeding (landfill) site

Figure 2 presents similar information on blows with the paws during spontaneous and feeding fights Like bites slaps and slashes during spontaneous fights were most often made to the area of the ruff Although slaps were much more common during spontaneous fights than in feeding disputes these blows seldom produced damage Slashes however tended to involve rump and back areas of the opponent a distribution which was closely paralleled by the distribution of the long raking wounds and scars observed on the back or rump of several bears The wounds produced by such slashes were by no means negligible one bear of the older colony a male in very poor condition was suffering from a deep gash on the rump This gash had been made prior to the beginning of observations and it showed no sign of healing over the observation period

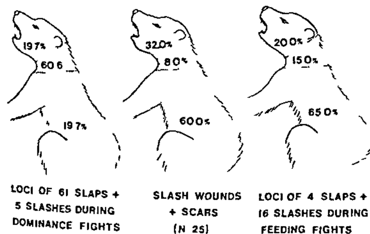



Fig 2 Slap and slash loci during feeding and spontaneous (dominance) fights.

## Determination of Dominance Relationships

Observations of the abilities of specific animals to obtain food which had fallen between 2 or more bears using a methodology similar to that of Masatomi (1964) enabled an assessment of relative dominance for many of the bears in each colony In the adult colony a straight line relationship was determined for the top ranking 5 colony bears with the exception that the relative dominance of 2 bears (numbers 3 and 4 of this 5 bear group) was uncertain All of these bears were males The 4 top ranked animals were all nearly equal in size and were by far the largest bears in the colony In contrast the fifth ranked bear was much smaller smaller in fact than 3 other males in this same colony all of which remained almost totally noncombatant running from any of the dominant animals This pattern of findings is in good agreement with Stonorov and Stokes (1972) report that size is related to dominance and that the most dominant animals in a free ranging group of Alaska brown bears were all male

A very similar situation was seen in the younger colony in which the top ranked bear was followed by 2 almost equally large males for whom relative dominance was difficult to assess Both of these animals were clearly more dominant than the animals ranked 4 and 5 in this group A much smaller male occupied the sixth position Due in part to the large number of animals in each colony dominance relationships were difficult to analyze for the remaining animals However a further attempt was made to assess dominance for 8 additional animals of the younger colony in order to determine the relationships between dominance and the many spontaneous fights in this group (many spontaneous fights were also seen in the older colony but these always involved the same group of 5 animals)

## Dominance Relationships in Spontaneous and Feeding Fights

As Table I indicates only 5 bears from each colony were filmed during spontaneous fights These were the 5 top ranked bears from the older group and 4 of the 6 top ranked animals from the younger colony Two top ranked bears from this latter group (numbers 4 and 5) did not participate in the filmed spontaneous fights although they were observed in spontaneous fights which were not filmed Also one lower ranking bear from the younger colony was filmed during these fights It might be noted that this animal suffered an upper palate and snout deformity which appeared to cause him considerable pain This factor may possibly have contributed to the apparent irritability of this bear which frequently nipped at or otherwise solicited fights with the other bears

These data indicate that the spontaneous fights are largely restricted to the top ranking males and suggest that one function of such fights may be to determine or maintain the dominance relationships among these animals If this view is correct then it seems likely that the majority of such fights should be between animals for which there is less certainty concerning relative dominance and that

this should be especially true for the longer and more vigorous fights In terms of such a notion it is interesting that in the older colony where dominance relationships might be expected to be more stable only the 5 top ranked bears were ever seen in spontaneous fights In the younger colony however a total of 14 of the 17 bears were observed in spontaneous fights although for the smaller and lower ranking members of this group such fights were extremely rare Since these animals were still in a period of rapid growth and since their experience of each other was considerably less than that of the bears in the older colony a finding of more spontaneous fights is completely consonant with the notion that dominance is under assessment in the spontaneous fights

In order to further assess this hypothesis all 14 animals in the younger colony which had been observed in spontaneous fights were ranked If each of these 14 animals fought each other bear of the same group of 14 in a round robin and the absolute rank differences for all fights were calculated for each animal a median rank difference of 4 should be obtained for the 8 animals in the center of the hierarchy of 14 while the 3 top and 3 bottom animals would have a median rank difference of 5 6 or 7 for their series of fights

For the 39 fights actually observed for these animals average rank differences were calculated for each combatant and compared with those expected for a subject of that rank The result was that 12 of the 14 bears fought with animals closer to their own rank than would be expected on the round robin fights model while 1 bear tied and one exceeded the predicted rank difference This deviation from the round robin model was significant (binomial test $p <$ 0 002) Thus the spontaneous fights appear to involve animals of closely adjacent rank more often than would be expected by chance

Further of the 39 spontaneous fights seen in this colony 12 were either 5 minutes or more in length or were described at the time of observation as "vigorous When these 12 fights only were analyzed in terms of the relative ranks of the combatant animals the average absolute difference in ranks was 1 91 as compared to a difference of 3 03 for all spontaneous fights and a difference of 4 85 as predicted by the round robin model This finding indicates that the most intense spontaneous fighting is among animals of adjacent ranks or perhaps for animals for which the relative ranking is still unclear

Recent views of the ritualization involved in conspecific fighting in many species suggest that the types of blows given and the target sites on the body of the opponent at which the blows were aimed evolve in order to permit a form of fighting in which there is relatively little danger of lethal wounding (Geist 1970 Blanchard Fukunaga Blanchard and Kelley 1975) It is clear that the spontaneous fights seen in Japanese brown bears meet both of these criteria The specific acts of wrestling and pinning of opponents plus the aiming of bites and blows at the well protected ruff area fit precisely such a model of low danger conspecific fighting while the length and form of the fight still permit assessment of strength and endurance Finally such fights occur more often

between closely ranked animals especially the longer and more vigorous spontaneous fights For these reasons the term dominance fight may be more appropriate than the designation of these encounters as spontaneous

Much the same reasoning applies to analysis of another possible interpretation of these fights that they represent play fighting One rationale for this interpretation is that such fighting is somewhat more frequent in young bears however as the present data make clear it is also found at a very high level in some fully adult bears Moreover although more of the younger colony animals participated in such fights than in the older colony this outcome is also logical in terms of the view that the major function of such fighting is to assess dominance Certainly the finding that the large and higher ranking male bears of each colony were much more likely to participate in these fights than the smaller (and perhaps younger) animals is less compatible with a play fight than with a dominance fight interpretation

An additional problem with the interpretation of spontaneous fighting as play is that play itself is often regarded as reflecting a preparation for some related activity when that activity becomes appropriate Thus play copulation might be regarded as practice for actual copulation when sexual maturity is achieved In this context it is clear that play fighting could be viewed as a preparation for the serious fights involved in disputes over food or possibly over a female or other disputed objects However this view is seriously contraindicated by the extreme difference in the topography of fighting during spontaneous or play fights as opposed to the food fights for which they are presumably a preparation

If the view that spontaneous fights are related to dominance is tentatively accepted the question then arises of the relationship between the form and target limitations for this type of fighting and that of dominance fights among free ranging male brown bears One problem in this area is that almost all congregations of wild brown bears are at feeding sites such as salmon rich rivers or landfill or garbage dump areas Thus the distinction between a dominance fight and a food dispute may be difficult to make in these circumstances *There have* been no systematic attempts to differentially describe dominance as opposed to food dispute fights in free ranging bears but a number of reports (cf J Craighead s report in Stonorov and Stokes 1972 that fights between dominant males involve especially severe wounding in the neck and shoulder region) suggest that some topographical differences in such encounters may be detectable

It should be noted that the circumstances in which the present bears are maintained may be so different from those of free ranging bears as to produce dominance fights more frequently than they occur under more natural conditions One possible reason may be the lack of space available for the establishment of territories in the bear park In this context the only example of exclusive use of a facility observed in these bear groups was that the dominant animal in the older group frequently used a dead tree trunk as a back scratching

post while no other animal in the group did so A related factor may be that free ranging male bears are sufficiently solitary so as to generally fail to meet unless some utilizable object (food sexually receptive female etc ) is serving as an attractant Thus since most male-male agonistic encounters may be partly or even primarily based on resource motivations the pure dominance fight may be extremely rare Even if this analysis is correct however the fighting topography and target sites associated with dominance fights may occur to a much greater degree in some agonistic encounters of free ranging male bears than in others Thus the present analysis suggests differences in the form of male fights depending on the circumstances in which the fights occur Finally the present results and analysis add to an increasing body of data (cf Geist 1971 Blanchard et al 1975) indicating that many animal species have complex patterns of intraspecific agonistic behavior which combine use of different weapon systems with specific acts and selection of targets on the opponent animal such that maximal information may be obtained without serious risk of damage during the fight

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AGGRESSIVE BEHAVIOR
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# Rhesus Plasma Cortisol Response at Four Dominance Positions

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Adrenocortical function and social behaviors were measured in 48 laboratory born juvenile monkeys in stable (original) groupings at rest in the same groupings in competition for drinking water in newly formed groupings each composed of animals from the same original dominance position and upon return to the original groupings, always in groups of four In newly formed groupings plasma cortisol measured higher with each step down in the new dominance hierarchy the effect attenuating by day 8 Although the partial correlation between frequencies of hostility behavior and plasma cortisol level was low (r = 0 05) when holding fear constant the partial correlation between cortisol and fear behaviors holding hostility behavior constant, was 0.86 The data provide evidence that corticosteroid elevations during social stress are related to behavior suggestive of fear and not aggression and are dependent upon dominance rank the level of dominance competition and previous dominance history

Key words social behavior dominance 17-hydroxycorticosteroids

## INTRODUCTION

Psychological stress associated with dominance hierarchies and measured by adrenocortical responses has been much more extensively investigated in subprimates than in monkeys (13) In general adrenocortical activity was found to be greater in subordinate rats and mice than in dominant animals (1 9) and appeared to be time dependent (12) since plasma corticosterone levels were increased in both dominant and subordinate mice at 6 hours but only in the subordinate mice at 24 hours Even subordinate animals may eventually adapt since

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subordinate chickens exhibited increased adrenal weights only when placed with unfamiliar chickens (17)

These results suggested that dominance stress would likely be strongest just after group formation affecting both dominant and subordinate subjects and would likely decline with increasing time spent in the group although more slowly for the subordinates Sassenrath (16) found response to ACTH injection a better correlate of social stress than 24 hour poststress urinary corticoids dominant males showed the lowest adrenal response subordinate the highest She concluded that plasma corticoid response to exogenous ACTH parallels behavioral measures of subordinacy and fear more closely than dominance rank Using plasma cortisol collected immediately after social experience we have shown social behavior particularly submissive behavior to be a better correlate of stress than other behaviors or dominance rank (6) the study in a within subjects design used monkeys whose dominance rank could be changed relative to the other group members Conversely Hayama (10) found *dominant* subjects in the monkey (Macaca irus) to have the heavier adrenal glands when caged in groups of 10–26 animals for 43–80 days in rather unusual circumstances This implied that dominance adrenocortical relationships might change with the duration of group experience [also suggested by the work of Candland and Leshner (5) on the relatively nonaggressive squirrel monkey] or the degree of crowding or might be different in monkeys compared to rodents although this last possibility would appear to be unsupported by other studies of the monkey (13) Accordingly the present study examined adrenocortical function in the monkey over a sufficient range of group durations to determine the time course and extent of adaptation to this social stress In addition the degree of crowding was held constant by experimenting with already available groups of four monkeys caged together under standard conditions and practices of animal care in our laboratory

Research with monkeys also offered a chance to explore behavioral parameters of social stress Intuitively the major source of stress for subordinate subjects would seem to be the threat of harm from those more dominant In this respect crowding produced increased adrenal weight in aggressive but not in nonaggressive strains of mice (4) Furthermore the act of fighting or being wounded has not itself seemed to be the main source of stress since both dominant and subordinate subjects (mice rats or chickens) appeared similar in the amount of fighting and being wounded whereas only the subordinate subjects exhibited heavier adrenal glands (9 17–19) or higher plasma corticosterone levels (12) Finally subordinate mice merely exposed to trained fighting mice developed heavier adrenal glands even though actual fighting was prevented (4)

To differentiate the kinds of dominance behaviors associated with stress in the monkey the present experiment measured frequencies of hostile fear and

positive behaviors as well as distances between animals In addition plasma cortisol concentrations were determined by a highly specific assay procedure (3) to provide a direct and rapidly responsive index of adrenocortical activity

## METHOD

### Subjects

The subjects were 35 male and 13 female laboratory born monkeys Macaca mulatta at 2–4 years of age They had been reared with daily social experience and maintained on 15 hours of light and 9 hours of darkness daily The e 48 animals were run in three successive replications At the beginning of the experiment the 16 monkeys of each replication had been living for the previous 9–33 months in four original groups (OG) of four animals each confined in wire mesh cages measuring 0 66 X 0 76 X 1 47 m for the older larger animals and 0 49 X 0 61 X 1 28 m for the younger smaller ones Animals were accustomed to handling and blood sampling as they had been used as controls for experiments on dietary abnormalities (8)

### Design and Procedure

In each replication the monkeys were first tested in their OG to obtain measures characteristic of long durations in the same group Testing consisted of the sampling of blood at 9 00 AM and 3 30 PM for cortisol analysis and the recording of behavioral categories as described below This day was termed day 0 Subsequently the OG dominance ranks were determined from two sessions in a water bottle dominance test (WBDT) In this test subjects were fed then deprived of food and water for 23 hours after that food was given and then 5 minutes later a single water bottle was introduced The elapsed time for each animal to accumulate 30 seconds of drinking time was recorded on electric clocks and the subjects were then ranked in dominance from 1 to 4 according to the order of increase of these elapsed times On the first WBDT only which lasted 60 minutes blood samples were obtained before (at 2 30 PM) and after (at 3 30 PM) the test and behavioral observations were recorded throughout On the subsequent Monday (day 1) beginning at 7 30 AM the subjects of each replication were taken from their four OGs and regrouped into four new groups (NG) each consisting entirely of strangers and were housed in the original colony room in unfamiliar cages which were however similar to the animals home cages Each of the four NGs consisted exclusively of the four subjects that had held the identical dominance position in their four OGs ie the four OG No 1 (dominant) monkeys were placed together in one NG the four

OG No 2 monkeys were similarly grouped together etc On days 1 2 4 and 8 of the NG condition blood was sampled at 9 00 AM and 3 30 PM and behavioral observations were recorded as described below On days 3 and 7 the groups were run in a WBDT solely to determine the NG dominance positions Finally at 7 30 AM on day 9 the subjects were removed from the NGs and were returned to the original groupings (ROG) in their original home cages Blood was sampled at 9 00 AM and 3 30 PM and behavioral observations (see below) were recorded On day 10 a WBDT confirmed that all monkeys had reestablished their old OG dominance positions

Blood samples of 0 5 ml each were obtained by allowing the monkeys in each group to enter transport cages from which they were immediately caught held by hand and bled from the saphenous vein into a 1 ml syringe containing dry heparin Blood was centrifuged within 15 minutes and the plasma frozen Assay was done by a protein binding procedure which measured only cortisol in normal monkey plasma (3)

Behavioral observations were adapted from those previously described by Kaufman and Rosenblum (11) and consisted of categories of the following a) positive behaviors including social and solitary play social grooming and clinging b) hostility behaviors including intimidation threat approach (when accompanied by withdrawal of the other animal) attack and pursuit c) fear behaviors including fear grimace crouch rigidity withdrawal flights and scream [see Chamove Eysenck and Harlow (7) for a rationale for this particular clustering] For each 15 second interval of an observation period a single tally mark was entered in each behavioral category for which one or more instance occurred In addition distances between subjects were estimated every 60 seconds by recording the grid positions of the subject – each cage was divided with tape markings into a 4 X 4 X 8 grid array of cage areas Behavioral observations for sampling times of 5 minutes or more were recorded at random intervals between 9 00 AM and 3 00 PM and respectively totaled 24 70 40 24 24 and 28 minutes for the following six experimental days day 0 of the OG condition days 1 2 4 and 8 of the NG condition and day 9 of the ROG condition As noted above 60 minutes of behavioral observations were also obtained during the first WBDT For analysis all behavioral observations were converted to frequencies per 24 minutes the smallest daily cumulative observation time

**Statistical Tests**

Analyses of variance (anovas) were used to test for group differences among the 4 X 4 factorial conditions of OG and NG dominance ranks with days as a repeated measure for analysis of the behavioral observations and both days and hours as repeated measures for the analysis of the plasma cortisol concentrations For each of the two dependent variables of plasma cortisol levels and

interanimal distance measures three separate anovas were done one on the OG and ROG conditions one on the WBDT condition and one on the NG condition Four separate anovas were done two on the WBDT and the ROG conditions and two on the NG condition two utilizing the frequencies of fear behaviors and hostility behaviors and two using the three positive behaviors During the OG condition all of these behaviors were too infrequent for statistical analysis

## RESULTS

### Plasma Cortisol Concentrations

OG tests After 9–33 months of living together in the original groups the subjects had cortisol levels (Fig 1) averaging 22 1 μg% (ie μg per 100 ml of plasma) Upon return to the same original groupings (ROG) after the NG condition these values were significantly higher 26 9 μg% F (1 32) = 13 68 p <

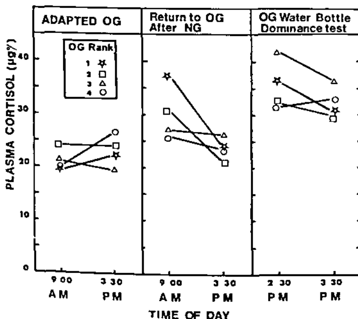



Fig 1 Mean plasma 17-OHCS values at two periods in the day in the original group situation, as a function of current dominance rank on day 0 day 9 and on the day of the Water Bottle Dominance Test

0 001 demonstrating a mild stress response most probably induced by the intervening new group situation There was no significant diurnal change in cortisol during the OG condition the 9 00 AM to 3 30 PM values being 21 2 to 23 1 μg% respectively for day 0 (F was nonsignificant) whereas an apparent diurnal change of 30 4 to 23 6 μg% occurred on the ROG condition F (1 32) = 17 27 p < 0 001 However this latter change appeared likely to reflect 9 00 AM increased levels of cortisol in the OG No 1 and No 2 subjects as a stress response one hour after the beginning of the ROG condition

In the OG Water Bottle Dominance Test the mean plasma cortisol value was 36 μg% at 2 30 PM after 23 hours of water deprivation and it declined significantly to 32 μg% at 3 30 PM after drinking and competing for water F (1 44) = 9 70 p < 0 01 These values compared to the lower OG values suggest stresses apparently due both to water deprivation and to dominance competition

NG tests Overall the plasma cortisol concentrations measured higher with each step down in the dominance hierarchy being 24 29 33 and 35 μg% for NG ranks 1–4 respectively F (3,32) = 3 91 p < 0 05 The magnitude of this inverse cortisol-dominance relationship as can be seen in Figure 2 varied from day 1 to day 8 the F for the interaction (9 32) being 2 24 p < 0 05 It was greatest on day 2 on which the NG No 4 monkeys failed to show any statistically significant adaptation to the new group situation compared to monkeys in the other NG ranks and it was smallest on day 8 on which the NG No 3 and 4 ranks were still above the range of adapted OG cortisol values whereas both the No 1 and 2 ranks were within the adapted range

The above inverse cortisol dominance effect in NG ranks was consistent over OG ranks and largest for animals of OG No 1 and 2 ranks and was least consistent for those of OG No 4 rank (Fig 3) F (9 32) = 2 21 p < 0 05 an effect not interacting with hours This correlated with the high level of vigorous dominance competition (see below) in those NG cages exclusively housing either OG No 1 or OG No 2 subjects

In addition there was a diurnal rank effect by dominance in the NG condition F (3 32) = 3 07 p < 0 05 The OG No 1 subjects caged together during the NG condition exhibited the highest 9 00 AM to 3 30 PM diurnal effect 38 to 31 μg% the OG No 4 subjects were next highest 32 to 28 μg% the OG No 2 subjects were next 31 to 28 μg% and the OG No 3 subjects were lowest 28 to 27 μg% Over all monkeys combined the average 9 00 AM minus 3 30 PM cortisol changes on days 1 2 4 and 8 of the NG condition were in order +9 +8 0 and 1 μg% F (3 96) = 9 86 p < 0 001 Thus all of the NG groups exhibited diurnal changes on days 1 and 2 which mostly adapted by days 4 and 8

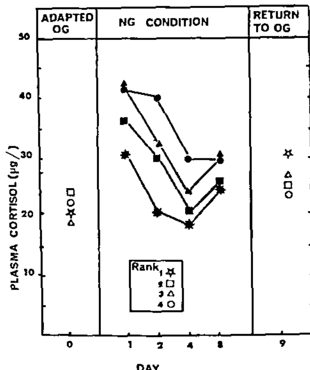



Fig 2 Plasma 17-OHCS levels in original and in new groups as a function of current dominance rank. Shaded area indicates adapted original group range

### Behavioral Measures

Distance and positive behavior Monkeys maintained average distances of 0 40 and 0 52 m apart respectively in the OG and ROG conditions F (1 16) = 16 59 p<0 01 and 0 63 m apart in the intervening NG condition Of interest if distance is considered to be a measure of group cohesion is the fact that the distance measures are related to the overall cortisol measures for the OG NG and ROG conditions On days 1 2 4 and 8 of the NG condition the OG No 1 subjects caged together exhibited distances suggestive of adaptation namely 0 72 0 72 0 66 and 0 49 m apart whereas the occupants of all other OG ranks who averaged 0 67 0 50 0 70 and 0 60 m apart exhibited no obvious adaptation trend (see OG Dominance Rank X Day F (9 96) = 5 29 p<0 01) Positive behaviors of cling groom and play summed together had a frequency of about 0

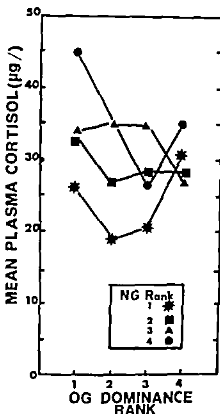



Fig 3 Plasma 17-OHCS over the eight days of the new group condition as a function of the interaction of the prior original group and current new group dominance rank

per 24 minutes in the adapted OG condition of 0 7 in the OG WBDT of 0 8 in the NG condition and of 1 6 in the final OG condition The OG WBDT and final OG conditions differed significantly with $F(1,32) = 9.28$ $p < 0.01$

The correlation between day 3 and day 7 dominance positions was perfect

*Hostility and fear behaviors* *There was a strong inverse relationship between* hostility and fear behaviors at different dominance ranks during the behavioral competition engendered by the OG Water Bottle Dominance Test but this relationship almost disappeared when the monkeys were returned from the NG conditions to the less competitive and more adapted ROG condition (see left and right panels of Fig 4) $F(3,32) = 17.64$ $p < 0.001$ The inverse relationship also held during the competition of establishing new dominance ranks during the NG condition (see middle panel of Fig 4) $F(3,32) = 14.85$ $p < 0.001$

By far the most hostility and most fear behaviors during the NG condition were exhibited by the higher ranked OG No 1 and OG No 2 monkeys who also

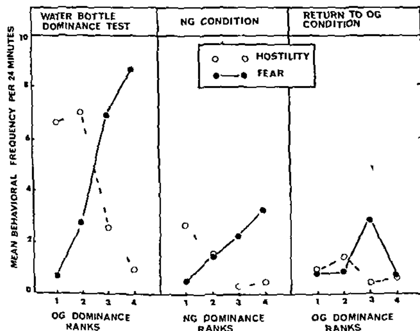



Fig. 4 Mean frequency of two behaviors (correlation with one another = −0 52) as a function of current dominance rank

showed an orderly relationship between their NG dominance rank and the frequenci s of these categories of behavior (Fig 5) these behaviors were less frequent and less orderly among the NG ranks of more subordinate OG No 3 and OG No 4 monkeys $F(9,32) = 2\ 83$ $p < 0\ 05$

The relationships depicted in Figure 5 were pronounced on day 1 were less so on day 2 and were weak and less consistent both on days 4 and 8 the interaction being $F(27\ 96) = 2\ 60$ $p < 0\ 01$

## DISCUSSION

On each of the first few days following the formation of new groupings of monkeys there was a clear inverse relationship between dominance position and plasma cortisol levels ie the more subordinate an animal the higher his cortisol concentration This supports similar findings in the squirrel monkey (5) using pooled 4-day poststress urine 17-OHCS Although thi effect declined considerably by day 8 following new group formation some was remaining the most dominant were still lowest and the most subordinate were still highest in their cortisol concentrations (Fig 1) In groups together for many months there

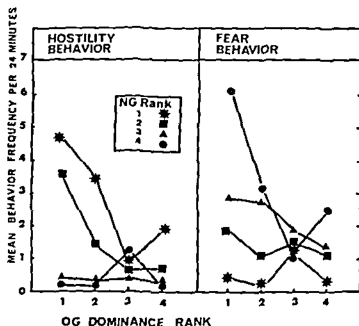



Fig 5 Mean frequency of two agonistic behaviors as a function of both prior original group and the current new group dominance rank over the eight days of the new group condition.

were no significant differences in mean plasma cortisol concentrations between monkeys in different dominance positions This is counter to the above mentioned results (5) using squirrel monkeys All animals were clearly stressed on day 1 of new group formation but the most dominant animals returned to low cortisol levels by day 2 the No 2 animals adapted by day 4 and the No 3 animals appeared adapted on day 4 but stressed somewhat again on day 8 and the No 4 animals adapted most slowly

As a curious aside on the adrenocortical responses of monkeys in groups the subjects generally failed to exhibit the expected diurnal cortisol decline from 9 00 AM to 3 30 PM Diurnal cortisol declines have been well documented in man and monkey and data (14) have indicated monkey cortisol values of 26 and 21 μg/100 ml at 9 00 AM and 3 30 PM respectively [these cortisol values were calculated by us after Bowman (2) as 80% of the 17-OHCS values reported elsewhere (14)] The expected diurnal decline did appear in the present study on days 1 and 2 after new group formation However the decline on day 1 most likely reflected a greater stress at 9 00 AM consequent upon formation of the group 1 hour earlier and there may have been some renewal of this stress on day 2 after the lights were turned on in the morning At any rate on days 4 and 8 when considerable cortisol adaptation had occurred the diurnal declines were

again absent Reasons for this absence remain to be investigated although we suspect that the daily occurrence of feeding at about 3 30 PM in our laboratory accounts generally for the present failure to observe lower cortisol values at 3 30 PM than at 9 00 AM

Comparison of cortisol changes with behavioral measurements for the various dominance positions in this study offered some insight into the course of stress associated with dominance In the first place the differences in cortisol concentration noted between the NG dominance positions was greatest in groups made up of previously all No 1 or No 2 monkeys (Fig 3) which were the same groups in which the dominance positions differed most in the exhibition of hostility and fear behaviors (Fig 5) Thus adrenocortical differences between dominance positions were greatest in those groups exhibiting the most dominance related behaviors Secondly the mean frequencies of fear behaviors noted for the *treatment combinations of old (OG) and new (NG) dominance positions* (Fig 5) varied in striking parallel with the corresponding cortisol concentration (Fig 2 middle panel) and accounted for 80% of the mean cortisol variance Pearson $r(14) = 0\ 89$ $p < 0\ 01$ Conversely the inverse relationship between mean hostility behaviors (Fig 5) and mean cortisol concentrations (Fig 2) was relatively low Pearson $r(14) = -0\ 44$ $p < 0\ 05$ Thus taking the partial correlation of mean cortisol and fear behaviors holding mean hostility behaviors constant gave an $r(12)$ of 0 86 $p < 0\ 01$ whereas taking the partial correlation of mean cortisol and hostility behaviors holding mean fear constant gave an r of only 0 05 The indications were thus clear that the bulk of the mean cortisol concentration was related to the mean frequency of fear behavior in the social dominance situation and not at all to the mean frequency of hostility behavior

These observations were consistent with studies discussed earlier employing subprimate species and various measures of adrenocortical response Establishing all of these features in one study with one species using a direct measure of blood cortisol concentrations strengthens the generalization that animals in all dominance ranks are stressed by new group formation but that the stress is greater and adaptation slower in animals that become subordinate Although after months of group living adaptation in terms of overall steroid level appeared statistically as good in the most subordinate subjects as in occupants of other dominance ranks marginal differences continued to exist between the No 4 monkeys and all others both in diurnal cortisol changes and in their plasma cortisol elevation in reaction to one hour of competition for water in the WBDT This suggested that some stress might still remain even after long adaptation for animals in the most subordinate position and that the lowest ranked animals perhaps should not be lumped with all others below the dominant as is often done

Finally the behavioral data provide strong evidence that corticosteroid elevations during social stress were related to behaviors suggestive of fear reactions

and were not related to emotional states accompanying the initiation of aggressive behaviors This supports work using the rodent (4) and the monkey (13 6) that indicated that the emotional threat of being attacked was a major source of stress in dominance situations This relationship was also broadly consistent with data from avoidance conditioning studies suggesting that adrenocortical stimulation is related to fear (6) and to a multitude of studies in the human that have related excess adrenocortical output to life situations that involve fear or anxiety (6 20)

However this last generalization was clear mainly for the new group condition Upon return to the original groups (ROG) the most dominant monkey in each grouping had the highest cortisol increase as if their fierce dominance competition during the NG condition in which most of them experienced subordinate roles had instilled some uncertainty regarding the divine right of kings This stress in the dominant animals was not accompanied by increased fear behavior however there was an almost complete lack of hostility behavior in these animals which was notably at variance with their previous dominance behavior in both OG and NG situations (compare the panels of Fig 4) Rowell (15) has summarized earlier data on dominance adrenocortical relationships as favoring an association of adrenocortical responsiveness with subordinance behaviors and subordinance ranks and in fact suggested that monkeys with greater adrenocortical responsivity are precast for subordinance roles Our main results are certainly consistent with the correlative portion of Rowell s thesis However contrary to Rowell s position even the most dominant monkeys in the NG condition exhibited stress levels of plasma cortisol on NG day 1 and the OG No 1 monkeys were only monkeys showing stress levels of plasma cortisol upon return to the original groupings (ROG) indicating that adrenocortical responsiveness is not exclusively related to subordinance behaviors or subordinance roles Social experience (or in a broad sense learning) as proposed by Rowell clearly played a role in this last finding although perhaps not exactly in the sense suggested by Rowell In our study therefore dominance stress not surprisingly appeared to depend upon a multiplicity of factors including dominance rank the level of dominance competition and previous dominance history

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AGGRESSIVE BEHAVIOR
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# Population Growth and Social Structure of Confined Colonies of Mongolian Gerbils. Scent Gland Size and Marking Behaviour as Indices of Social Status

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Male gerbils have larger ventral scent glands, and they mark more than females. In both sexes scent gland activity is dependent on gonadal hormones. Observations on colonies of gerbils, living in enclosures or cages, showed that both scent gland size and marking behaviour were related to social status In colonies founded by a single pair breeding was confined to the original female The infertility of the daughters was due to failure of sexual maturation. As this was always associated with a lack of development of the scent glands, the functional state of the latter could be used as an index of fecundity A change in social organization (eg removal of the parents) caused previously infertile females to conceive and was accompanied by development of the scent glands. If there was competition for dominance the scent glands of the losers regressed at autopsy their ovaries and uteri appeared to be nonfunctional. The founding father usually had a larger scent gland than his sons but the inhibition of sexual function was not as severe as in the females However the father characteristically showed much more marking behaviour in a neutral territory than his sons. None of the females—except the mother—showed appreciable marking and her scores were much lower than those of the dominant male Asymptotic populations were reached at about the same level in enclosures and cages implicating an intrinsic capacity for control independent of the number of animals per unit of space but probably related to the natural size of a social group Stabilization of numbers was achieved not only by reproductive inhibition of young females, but also by cessation of breeding by the founding mother and death of litters. Littermates raised in enclosures without their parents showed delayed sexual maturation accompanied by fighting which resulted in the formation of a hierarchy headed by a breeding female and a dominant (marking) male

Key words aggression gerbil marking behaviour population control, scent gland

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Rodents and other small mammals have a high reproductive capacity Under natural conditions different strategies are used to limit population size so as not to overexploit the habitat (Solomon 1949 Wynne Edwards 1962 Myers et al 1971) The *efficiency of the control systems varies* so that some species particularly those which live in subarctic habitats such as lemmings (Marsden 1964 Clough 1965 1968) and voles (Chitty 1960 Bujalska 1973) show large cycli fluctuations a population peak being followed by a crash and then a gradual build up while others eg deermice show very little variability from season to season (Terman 1973 Sadleir 1965) Mice and rats seem to be in between (Brown 1973 Christian 1971 Myers and Krebs 1974) The different self regulatory mechanisms used by various species of rodents have been extensively investigated (for reviews see Archer 1970 Brain 1971 Calhoun 1963 Christian 1971 Christian and Davis 1964)

Under laboratory conditions all extrinsic limiting factors (climate predation food shortage) can be eliminated so that stabilization of a *freely breeding* population must be accomplished through social controls These fall broadly into two categories (1) inhibition of reproduction and (2) death of infants and juveniles. Comparative studies of different rodents have shown that the strategies used in captivity reflect those in the wild Thus species such as rats that live in colonies under natural conditions may increase in numbers for several generations in captivity before population growth is curtailed (Southwick 1955a b Crowcroft and Rowe 1958 Lloyd and Christian 1969) At the other extreme is the golden hamster believed to live a solitary existence in the wild In a previous study in this laboratory colonies of golden hamsters founded by two pairs and living in enclosures for several months never exceeded a total of eight animals (Goldman and Swanson 1975) This was the result of high infant mortality as both the founding females and their daughters were almost continuously pregnant but their litters were killed by conspecifics soon after birth

It has been claimed that observations on the behaviour of captive animals may have limited usefulness in understanding population control in nature Any general theory must apply both to natural and laboratory situations as long as it is realized that the regulating behaviour in any given species may vary according to circumstances One area in which the understanding of the structure of animal social groups and their interactions with the environment is of importance is that of plague and pest control (WHO 1974) Furthermore an appreciation of the social biology of a species extensively used in experiments particularly psychological studies is vital for a meaningful interpretation of results

The Mongolian gerbil has recently become a popular subject for behavioural studies (Schwentker 1972) The response of gerbils to the challenge of density regulation under laboratory conditions was therefore investigated using the same enclosures which had previously been used for hamsters (Goldman and Swanson 1975)

The few reports on gerbils living in their natural habitat (Mongolia and northern China) suggest that the animals live in colonies possibly in large family groups (Allen 1940 Bannikov 1954 Tanimoto 1943) Complex burrows are excavated in dry and sandy soil These may have several entrances and form a system of interconnecting tunnels up to 3 or 4 m long at various levels below the surface The gerbil retains its burrowing activity in captivity and will build simple tunnel systems if housed in an earth box (Solberg 1973 Clark and Calef 1977 and Swanson H)

On the subject of colony cohesion Marston (1972) reports that several consecutive litters can live together in harmony and that breeding is most successful if animals are permanently caged in monogamous pairs Agren (1976) observing the behaviour and breeding of gerbil populations housed in large outdoor enclosures during the summer months in Sweden reports that family groups remained together throughout the four months of study Family groups were therefore used as nuclei to start the colonies in the present investigations

## MATERIALS AND METHODS

### Housing Conditions

Enclosures The eight enclosures were in a room adjoining the main animal house They were divided by metal partitions and measured 90 × 80 × 60 cm The floor was tiled Each enclosure had a corridor system built of wire mesh which divided the floor space into compartments of varying sizes as shown in Fig 1 and described by Goldman and Swanson (1975) A balcony ran along one side of the enclosure room from which the enclosures could be surveyed To enhance observation mirrors were placed along the opposite wall so that any parts of the enclosures that could not be surveyed directly could be seen by their reflection

The enclosures were liberally supplied with sawdust which was changed every six weeks Woodwool was supplied for nest building The enclosures had a reversed lighting schedule and no natural daylight Red light was on from 10 00–24 00 hr each day and white fluorescent light for the remainder

All animals were given food and water in excess of their needs The food consisted of standard Thompsons pellets supplemented by mixed seeds and bread with Bemax carrots and cabbage given weekly

Cages All cages were standard transparent polycarbonate (Macrolon) 43 × 26 × 12 cm with a removable galvanized grill lid that held a food hopper and water bottle The cages were cleaned once a week and fresh sawdust was given with woodwool for nesting if a litter was present A typical crowded cage is shown in Fig 2



Fig 1 A typical colony of gerbils living in an enclosure

## Animal Identification

Each animal was identified by the letter or number of its enclosure or cage and its own number which was shown by an earmarking code All the original animals were marked at week 0 All animals born during the experiment were earmarked at 3 or 4 wk of age Earmarking was performed without anaesthesia

## Weekly Weighing and Measuring

Each week every animal involved in the experiment was weighed to the nearest gram The width and length of its scent gland were measured to the nearest millimetre using a ruler and the secretory scent gland was assessed according to an arbitrary scale of 0 to +++ In order to measure the gland the belly of each animal was shaved This procedure was carried out without anaesthetic by firmly gripping the animal by the loose skin over its neck and spine and using an electric clipper




Fig. 2 An asymptotic population living in a crowded cage

Records were kept of scars due to fighting and the general condition of the animals was noted. Pregnancies were also detected at these weekly weighings and if a birth seemed imminent the enclosure or cage was inspected daily to record the birth of a litter. Sleeping locations were noted once a week.

#### Marking Tests

The arena consisted of a circular area (diameter 55 cm) enclosed by a metal wall 28 cm high. The lino floor was marked into divisions and at intervals 18 plastic pegs (2 × 2 × 2 cm) were fixed to the floor which the animals used for marking. The arena was lit by two fluorescent strip lights (30 W) positioned 1.5 m above the apparatus.

Testing was carried out at intervals. Each enclosure or cage of animals was tested the same day. The arena was washed with detergent and water and dried between testing each enclosure or cage but not between testing each animal

Testing order was random Each test lasted 5 min and the number of times that an animal rubbed its ventral gland on a peg or on the floor was recorded After testing the animals were returned to their enclosure or cage

### Autopsy

All animals left at the end of each experiment were killed and various measurements and weights were recorded These included body weight dimensions of scent gland weight of excised scent gland weight of ovaries/testes and weight of uterus/seminal vesicles Histological sections were prepared of ovaries and uterus

### Statistics

Wherever appropriate means ± SEM were calculated and Analysis of Variance and Student s t tests were applied

## DESIGN AND RESULTS OF INDIVIDUAL EXPERIMENTS

### Experiment I Parents in Enclosures

The purpose of this experiment was to study population growth in colonies of gerbils founded by a single pair and housed in enclosures

### Experimental Design

Period A (Weeks 0–34) Eight established breeding pairs with their young were placed in separate enclosures Four pairs (Enclosures A–D) had a litter of juveniles (4–6 wk old) as well as infants while the other four only had infants

In this experiment the scent glands were measured only twice when the animals had been in the enclosure 20 and 34 wk All animals were tested for marking at 20 wk

*On several occasions individuals from one enclosure were placed in a strange* enclosure and the behaviour of the inhabitants to the intruder was observed for 10 min (or less if there was risk of injury) The intruders were systematically chosen to represent the father mother an adult and a juvenile of each sex

Period B (Weeks 34–44) Eleven adult brother sister pairs were removed from Enclosures A–F when they were 5–7 mo old and placed in separate cages for 10 wk In the remaining enclosures the effect of removing the mother was observed

**Results**

Period A  Only three of the eight founding mothers continued to reproduce after being placed in the enclosures  The reproductive pattern in the four en closures where breeding occurred is shown in Fig 3  The mothers in Enclosures A

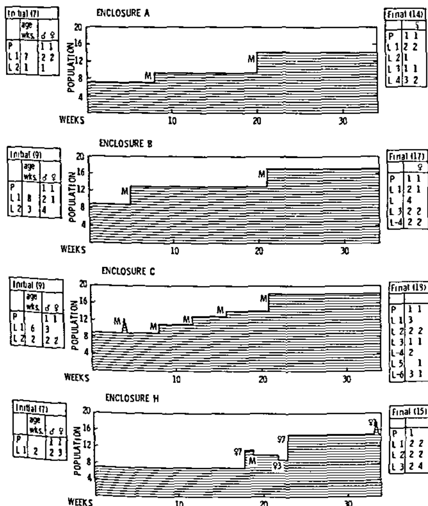



Fig 3  Experiment I  Population dynamics in colonies of gerbils founded by an adult pair plus one or two litters in enclosures.

and B produced two litters each with most of the young growing to maturity The mother in Enclosure C had five litters but many of her offspring died with in a few days of birth The pattern in Enclosure H was interesting The mother failed to breed and then died 18 wk after being placed in the enclosure It was not known whether she died of natural causes or whether she was killed Just before her death a daughter (No 7) produced a viable litter Two weeks after that her sister (No 3) was found dead and a week later female No 7 produced a second litter Thus No 7 became the breeding female

At the end of 34 weeks the total population in the enclosures where breeding occurred was between 14–18 animals Enclosures D–G where no breeding occurred contained founding population of 6–9 adults All surviving animals were in excellent condition

Throughout the experimental period there was much social interaction but mating was only seen between the mother and father usually at postpartum There was no overt evidence of fighting although it is not known what caused the death of the two females in Enclosure H Most animals slept together in the same nesting compartment throughout the period of study

A nursing mother with her infants usually isolated herself for a few days but then brought the infants to the communal nest Various individuals of either sex often sat with the pups in place of the mother

A striking observation was that while the parents were present none of the young females ever became pregnant even though they were well past the age of puberty In gerbils the ventral scent gland appears at puberty and is known to be influenced by gonadal hormones (Glen and Gray 1965 Owen and Thiessen 1973) No females showed any sign of scent gland development when they had been living in the enclosures with their parents for 20 wk they were then 21–6 weeks old By the end of the experiment 4 of 26 females had developed scent glands (Table I) but these were significantly smaller and less active than those of their mother As expected scent glands in males were larger than in females (Whitsett and Thiessen 1972) The age at which glands first appeared was not noted but although scent glands were present in all young males by the age of 21–26 wk they were significantly smaller and less actively secreting than the glands of their father (Table I) It was also observed that when they were 5–7 mo old the offspring were still significantly smaller than their parents (Table I) They were also smaller than other colony animals of the same age housed alone or in pairs

When tested in the arena seven out of eight fathers marked actively (Table I), and five of them continued to mark on being replaced in their own enclosure Neither sons nor daughters marked at all – two mothers marked less than five times each

When a stranger was introduced into an enclosure he was often – but not always – attacked by a resident The age and sex of the intruder did not seem to

**TABLE I Experiment I Fertility Scent Gland Development and Marking in Colonies of Gerbils Founded by a Single Pair and Living in Enclosures With Their Parents**

| | Females | | Males | |
|---|---|---|---|---|
| | Mothers | Daughters | Fathers | Sons |
| Total number | 8 | 26 | 8 | 29 |
| Scent gland | | | | |
| No with gland | 8 | 4 | 8 | 29 |
| Length (mm) + | 17 5 ± 0 4 xxx | *10 7 ± 0 2* | *25 6 ± 0 4 xxx* | *19 3 ± 0 8* |
| Marking | | | | |
| No marking | < 2 | 0 | 7 | 0 |
| Score | < 5 | | 30 1 ± 4 7 | |
| No breeding | 3 | 1 (After mother s death) | | |
| Body weight (gm)* (offspring age 24 wk) | 75 8 ± 2 9 xxx | 56 6 ± 1 4 | 73 3 ± 2 9 xx | 66 7 ± 1 8 |

*Mean ± SEM
x p < 0 05
xx p < 0 01
xxx p < 0 001

matter juveniles being attacked as frequently as adults The attack could be initiated by any individual not necessarily the father Once a fight started the mood seemed to be contagious and various residents were often seen fighting and chasing one another When the intruder was returned to his home enclosure he often started footstomping He was investigated by his cagemates and sometimes briefly attacked

Period B (Table II) After being placed in separate cages eight of the 11 pairs of previously infertile offspring started to breed producing 15 viable litters during a period of 10 wk None of the females had scent glands at the time of pairing but within a month all had large actively secreting glands The glands of their male partners also increased significantly

Of the females remaining in the enclosures after removal of their mother seven out of 10 developed scent glands and of these three produced litters The animals which did not breed were killed and their reproductive organs were weighed (Table III) and examined histologically The three females without scent glands had small immature ovaries without corpora lutea (CL) and an atrophic uterus in contrast to the functional reproductive tract seen in the four females with active glands

**TABLE II Experiment I Effects of Pairing of Offspring on Scent Gland Development and Fertility**

| | Females | | Males | |
|---|---|---|---|---|
| | Before | After | Before | After |
| Total No | 11 | 11 | 11 | 11 |
| Scent gland | | | | |
| No with gland | 0 | 11 | 11 | 11 |
| Length (mm) | – | 16 8 ± 0 7 | 16 5 ± 1 1 xxx | 26 4 ± 0 7 |
| No breeding | 0 | 8 | | |

xxx p < 0 001

**TABLE III Experiment I Weight of Ovaries and Uterus (Mean ± SEM) of Females With or Without Scent Glands**

| Animals | N | Ovaries with CL | Ovaries Wt (mg) | Uterus Wt (mg) |
|---|---|---|---|---|
| Without scent glands | 3 | 0 | 19 3 ± 2 3 | 51 0 ± 3 3 |
| With scent glands | 4 | 3 | xxx 48 6 ± 11 5 | xxx 154 0 ± 7 3 |

xxx p < 0 001

### Experiment IIa Parents in Cages

The purpose of this experiment was to ascertain what effect crowding (ie confinement to a small cage) has on reproductive performance litter survival and dominance and whether dispersal into a larger enclosure would alter the social structure

### Experimental Design (Weeks 0–34)

Three cages containing a breeding pair each with a litter of juveniles and a litter of infants were set up After 18 wk the inhabitants of each cage were dispersed into freshly cleaned enclosures At 24 wk the mother died in one enclosure and in order to standardize conditions the mothers from the other two enclosures were also removed

Marking tests were carried out at four intervals

### Results

**Population Structure (Fig 4)** Cage 1 The number of animals never exceeded the original number of 13 The mother had three litters in the cage and one in the enclosure which all died None of the daughters had scent glands until removal of the mother when all four developed glands and became pregnant None of their litters survived Fighting occurred between the father and two of his sons The father and one son were killed and the other son emerged as the highest marker

Cage 2 Until 14 wk only the original mother showed breeding activity her first litter survived raising the population to 19 animals a total that was never exceeded Her next two litters died She then stopped breeding and one of her daughters had one litter in the cage and two more in the enclosure none of which survived She was the only one of 11 daughters who had a scent gland prior to the removal of the mother After this event seven more females developed glands four of these became pregnant The father had the highest marking score although after removal of the mother two sons also had high scores

Cage 3 The first litter born to the original mother survived and raised the total number of animals to 17 a figure that was never exceeded She had three more litters in the cage and two in the enclosure but none survived Following the death of her fifth litter the mother was attacked for a fortnight and finally killed by the other animals Just before her death two daughters began to show glandular activity and finally four of eight had glands and three became pregnant

Again the father was the highest marker but one son showed an increase after the mother s death

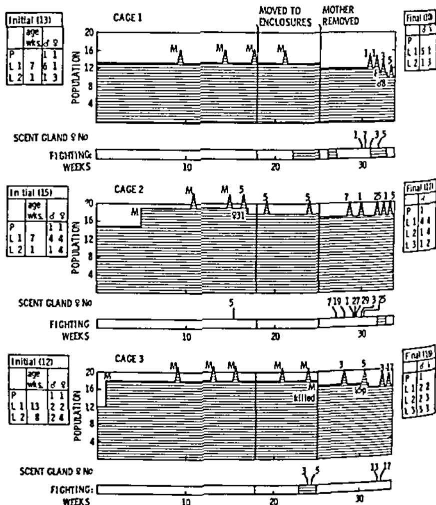



Fig. 4 Experiment IIa Population dynamics in colonies of gerbils founded by an adult pair plus one or two litters in cages

The results of this study showed that

(1) Although the mother continued to breed litters failed to survive once the population reached asymptote (in this case 13–19 animals)

(2) Dispersal to a larger area had no effect on the reproductive pattern

(3) The presence of the mother inhibited sexual development (mirrored by scent gland inhibition) in her daughters

(4) After removal (or decline) of the mother the daughters became reproductively active as shown by the development of glands and pregnancies

(5) In a stable family situation the father was the highest marker During the social reorganization which followed removal of the mother one or more sons showed increased marking This was sometimes accompanied by fighting and in one case resulted in the death of the father

**Experiment IIb Parents in Cages**

In this experiment the role played by the father and mother respectively on suppression of breeding in their daughters and scent gland marking on the sons was further investigated

**Experimental Design**

Period A (Weeks 0–34) Twenty established breeding pairs without young were placed in individual cages No young were removed from the cages throughout the duration of this study At the end of 24 wk all animals older than 15 wk were tested for scent marking in the arena

Period B (Weeks 34–44) Either the father or mother were removed from alternate cages which left ten cages containing only the father and offspring and ten cages containing only the mother and offspring One month later all animals were again tested for marking behavior

At 44 wk after the beginning of the study all females including the original mothers were autopsied

**Results**

Period A All 20 mothers bred (Table IV) each producing three to seven litters of which a maximum of five litters per mother (containing two to five young each) survived to maturity It seemed that as soon as cage density reached about 18 animals the mothers either stopped breeding or if they continued the litters died within 1 or 2 days of birth This appeared to be due to maternal neglect or to being trampled by cagemates cannibalism was not directly observed Although at the end of the experiment the animals were very crowded and therefore restricted in their activity they remained in excellent condition (Fig 2) there was no evidence of fighting prior to the removal of a parent

As in the enclosures and in Experiment IIa breeding was inhibited in most of the daughters only three of 83 became pregnant and their litters failed to survive (Table V) Scent gland development was not inhibited to the same extent as in the enclosures insofar as 29 of 83 females had glands but these were significantly smaller than those of their mothers The scent glands of sons were also significantly smaller than those of their fathers as was the body weight of

**TABLE IV Experiment IIb Growth of Populations Founded by Adult Pairs Living in Cages for 34 Weeks**

| Cage No | No litters | | Final |
|---|---|---|---|
| | Born | Weaned | population |
| 1 | 5 | 3 | 16 |
| 2 | 4 | 3 | 14 |
| 3 | 6 | 3 | 11 |
| 4 | 6 | 3 | 9 |
| 5 | 5 | 3 | 11 |
| 6 | 3 | 1 | 4 |
| 7 | 3 | 1 | 6 |
| 8 | 7 | 5 | 11 |
| 9 | 5 | 3 | 12 |
| 10 | 7 | 3 | 17 |
| 11 | 6 | 3 | 8 |
| 12 | 5 | 3 | 18 |
| 13 | 5 | 3 | 14 |
| 14 | 3 | 2 | 11 |
| 15 | 6 | 3 | 17 |
| 16 | 4 | 3 | 15 |
| 17 | 5 | 3 | 12 |
| 18 | 4 | 0 | 2 |
| 19 | 5 | 3 | 13 |
| 20 | 4 | 3 | 16 |
| Mean | 4 9 | 2 6 | 16 9 |
| Range | (3–7) | (0–5) | (2–18) |

the offspring of both sexes at the age of 24 wk The usual sex difference in scent gland size was noted

Incidentally at the same age neither body weight nor scent gland size in either sex varied between the first and subsequent litters born in each cage The presence of older siblings therefore did not have an additional inhibitory effect to the presence of the parents

When tested in the arena 90% fathers marked while only 16% sons marked Furthermore the marking score of the fathers was double that of the sons who marked Marking by females was much less frequent than by males but the mothers marked more than their daughters

Period B Removal of the mother had a profound influence on the daughters (Table VI) The scent glands began to grow in a proportion of young females which had not previously had glands (15 of 37 daughters had glands before re moval of the mother and this increased to 27 after removal) Furthermore 14 daughters became pregnant but probably because of the crowded conditions of the cages only four litters survived to maturity In four cages there was ev

TABLE V Experiment IIb Fertility and Scent Gland Development in Colonies of Gerbils Founded by a Single Pair Living in Cages With Their Parents

| | Females | | Males | |
|---|---|---|---|---|
| | Mothers | Daughters | Fathers | Sons |
| Total No | 20 | 83 | 20 | 67 |
| Scent gland | | | | |
| No with gland | 20 | 29 | 20 | 67 |
| Length (mm) | 19 5 ± 0 5 xx | 17 4 ± 0 3 | 28 7 ± 0 5 xxx | 24 0 ± 0 3 |
| Marking | | | | |
| No marking | 9 | 8 | 18 | 11 |
| Score | 10 0 ± 1 7 xxx | 4 9 ± 1 9 | 27 9 ± 0 4 xxx | 13 7 ± 3 8 |
| No breeding | 20 | 3 | | |
| Body weight (gm)* (offspring age 24 wk) | 82 9 ± 3 4 xxx | 52 4 ± 1 0 | 92 7 ± 3 6 xxx | 56 6 ± 0 9 |

Mean ± SEM
x $p < 0.05$
xx $p < 0.01$
xxx $p < 0.001$

dence of fighting after removal of the mother Scent glands sometimes regressed in females who had developed a gland The absence of the mother had no obvious effects on the sons

Removal of the father had no influence on the daughters but the proportion of sons which marked doubled although the scores were not significantly changed

### Autopsy Results

Females The age of individual females and the size and activity of their scent glands in the weeks previous to autopsy were used to place the animals into the categories depicted in Fig 5

(1) Prepubertal (age 10–16 wk)

(2) Inhibited (no scent gland at any time)

(3) Declining (scent gland previously active now inactive)

(4) Increasing (scent gland previously inactive now increasing) None of the above animals had been pregnant at any time

(5) Steady state nonparous (scent gland active)

(6) Steady state parous (including the original mothers) Animals pregnant at autopsy were not included in the results

(7) For comparison an additional group of ovariectomized females was added

**TABLE VI Experiment IIb Effects of Removal of Mother or Father on Fertility Scent Gland Development and Marking of Offspring**

| | Females | | Males | |
|---|---|---|---|---|
| | Before | After | Before | After |
| A Removal of mother | | | | |
| Total number | 37 | 37 | 25 | 25 |
| No with scent glands | 15 | 27 | 25 | 25 |
| No breeding | | | | |
| Litters born | 1 | 14 | | |
| Litters weaned | 0 | 4 | | |
| Marking | | | | |
| No marking | 4 | 0 | 3 | 3 |
| Score (mean ± SEM) | 2 5 ± 0 3 | | 3 6 ± 1 6 | 1 3 ± 0 3 |
| B Removal of father | | | | |
| Total number | 46 | 46 | 42 | 42 |
| No with scent glands | 14 | 17 | 42 | 42 |
| No breeding | | | | |
| Litters born | 2 | 3 | | |
| Litters weaned | 0 | 0 | | |
| Marking | | | | |
| No marking | 4 | 2 | 8 | 16 |
| Score | 8 0 ± 3 8 | 2 0 ± 1 0 | 17 5 ± 4 5 | 16 4 ± 3 0 |

The animals in the three groups without measurable scent glands all had small ovaries without corpora lutea (CL) and small atrophic uteri As there was no significant difference between the three groups the reproductive tract of the inhibited and declining animals was deemed to be similar to the prepubertal state The uterus was the same size as after ovariectomy the ovaries were therefore completely inactive

On the other hand the ovaries from groups 4–6 with active scent glands (whether or not they contained CL) were much heavier than those of animals with atrophic glands in groups 1–3 The lower mean ovarian weight in the steady state nonparous group in comparison with the other two groups probably reflects the smaller proportion of ovaries containing CL

The functional activity of the ovary is not necessarily associated with the presence or absence of CL since this parameter did not affect uterine or gland weight There was no significant difference in uterine weight between the three groups with active ovaries and scent glands The greater size of the glands in the

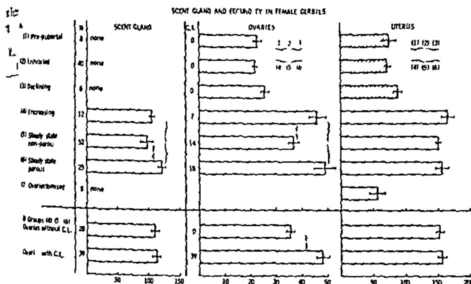



Fig 5 Experiment IIA and IIB The relationship between fecundity and scent gland size in female gerbils and the weights of the ovaries and uterus

parous group may reflect additional hormonal stimulation during previous pregnancies

In the present study both uterus and scent gland reflected endocrine secretion by the ovaries. The ventral scent gland is therefore a very useful external measure for accurate prediction of the functional state of the reproductive system in a dynamic social situation

*Males* The relationship between scent gland size and seminal vesicles shows a significant regression coefficient (Fig 6) Since both tissues are known to be testosterone-dependent this suggest that the size of the scent glands can be taken as a rough index of testosterone secretion In contrast to females however reproductive activity was not completely surpressed in any males and as scent gland size in males only varied over a small range this measure could not be used as a reliable index of testicular secretion

### Experiment III Parents Not in Enclosures

The first two experiments demonstrated an inhibition of sexual maturation in the offspring of established breeders In order to elucidate the role of the parents

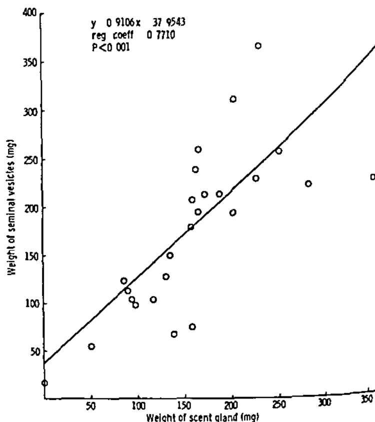



Fig. 6 Experiment IIb The relationship between the weights of scent glands and seminal vesicles.

breeding in littermate groups growing up together without parents was investigated

**Experimental Design**

Period A (Weeks 0–18) Either one or two consecutive litters born in cages were placed in the enclosures when they were 3–13 wk old Marking tests were carried out 10 and 15 wk after the beginning of the experiment

Period B (Weeks 18–35) By week 18 there was no sign of breeding even though the animals were now between 18–28 wk old and theoretically well past the age of puberty The inhabitants of four enclosures chosen at random were removed to cages in order to make room for the dispersal of the caged animals of Experiment IIa These animals will not be discussed further The remaining animals were left in the enclosures Their reproductive pattern from weeks 0–35 is depicted in Figure 7

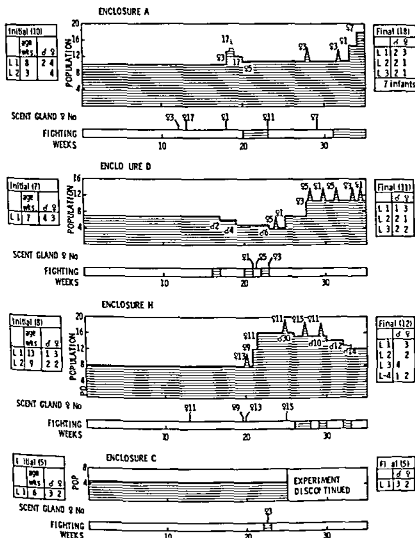



Fig 7 Experiment III Population dynamics in colonies of gerbils founded by one or two litters without parents in enclosures.

## Results

Period A This was a period of stability with no apparent social structure The animals in each enclosure habitually slept together In some cases the sleeping compartments stayed the same throughout the study in others it was altered

from time to time There was no fighting and animals were in excellent condition (Fig 1) No mating was observed there were no pregnancies and marking behaviour was minimal

Scent gland development was greatly delayed in animals of both sexes but especially in females In normal colony cages in which heterosexual pairs are established from weaning the scent gland first appears at the age of 5–6 wk in males and at 8–10 wk in females and the first litter may be born to 13 wk-old females In the present experiment scent glands did not appear in any male before the age of 7 wk and in many the first sign of a gland was delayed much longer Inhibition was almost complete in females insofar as only a single female had a gland by the age of 20 wk

Period B For no apparent reason a change occurred in the enclosures after 18–20 wk Several females now 25–32 wk old started to develop scent glands and some became pregnant The onset of sexual activity was accompanied by a period of marked social instability with much fighting involving animals of both sexes

The peaceful gregarious style of life seen during period A made all the more striking the disruption that occurred during this period of social reorganization Animals were now found isolated in all areas of the enclosure often two or three would aggregate at the top of a ramp and compete for places there If aggression were directed at one animal this individual would initially sleep with the group apart from bouts of fighting If aggression continued the physical condition of the animal deteriorated and it would be found isolated gradually getting weaker until it finally died On several occasions solitary females became isolated from the group and actively defended a compartment in the enclosure becoming more aggressive and leaving the compartment only to eat If another animal entered the compartment while the female was eating she returned immediately and there would be a violent fight resulting in her reoccupation of the area Other animals were threatened through the mesh Such a situation was accompanied by slow physical deterioration through wounding and starvation and finally terminated in death

Pregnant females were particularly vulnerable to attack This resulted in the establishment of one or two breeding females the remainder being either killed or inhibited (ie their scent glands regressed and at autopsy their reproductive organs were atrophic) At the same time one male usually emerged as dominant as shown by his high marking score when tested in the arena This sometimes involved the death of rival males Following the establishment of a relatively stable hierarchy peace was restored and the animals were again found interacting socially and sleeping in communal nests

Population structure The changes that occurred in the four enclosures whose inhabitants were not transferred to cages are illustrated in Fig 7

Enclosure A Females Nos 3 and 17 developed a scent gland and soon both became pregnant No 3 delivered a litter which survived but fighting broke out during which females Nos 17 and 5 were killed No 3 had two more litters which died and just before the experiment was terminated two more females successfully bore litters Again there was evidence of fighting There was one dominant male marking during this period

Enclosure D Several males marked in a test conducted shortly before a period of acute strife when three males were killed The marking score of the only surviving male rose sharply after this period At the same time three females showed reproductive activity Females Nos 1 and 5 had viable litters and then these two plus No 1 alternately produced litters none of which survived

Enclosure H Three females became pregnant at the same time and two had litters which survived At this time a single male was marking (No 10) Some weeks later there was a period of intense social upheaval when several females delivered unsuccessful litters and all four adult males were killed including No 10 Only juvenile males were left none of which marked

Enclosure C Although Female No 3 developed a scent gland there was no change in social structure or breeding by week 25 Two brother sister pairs were then placed in cages and both bred successfully

Thus each population showed a different structure in terms of the number of females breeding and the survival of their litters Reproductive success was limited due to one or a combination of following factors death of litters death of pregnant females and inhibition of breeding (accompanied by regression of scent glands) Even in enclosures where there were one or two successfully breeding females litters failed to survive once the population contained 12–18 animals

## Experiment IV Parents Not in Cages

In this experiment the effect of density was investigated by comparing the social structure of littermates (without parents) confined to cages to that of similar groups growing up in enclosures (Experiment III)

### Experimental Design

Seven cages were prepared containing one two or three consecutive litters aged 3–11 wk In addition 15 young pairs of the same age range were placed in cages

#### Results

Scent gland development followed a parellel course in littermate groups and pairs glands first appearing in males by 5–6 wk and being fully active by 10 wk In females glands first appeared at 9–11 wk and were fully developed by 13–15 wk

Furthermore in six of seven cages containing groups one or more females became pregnant at a very early age (Table VII) Thus 11 of 25 conceived between 13–18 wk of age and seven gave birth to live litters The others were pregnant when the experiment was terminated

By the time they were 15–23 wk old seven of 15 females living in pairs had borne litters The earliest conception occurred at 10 wk of age

It is of particular interest that the social structure of young animals growing up in cages differed markedly from that of similar animals growing up in enclosures In Experiment III there was an initial period of stability when sexual development was inhibited followed by a period of conflict when sexual maturation took place finally succeeded by a stable hierarchy None of this was seen when similar groups of animals were confined in a small cage In this instance sexual maturation followed a normal course ie similar to young pairs and there was little fighting although several females were pregnant concurrently The further progress of these groups was not followed so it is not known what the final social and population structure would have been

### GENERAL RESULTS

#### Inhibition of Scent Gland Development (Fig 8)

The age at which a scent gland first appeared and its subsequent rate of development was influenced by the social conditions in which the young animals were reared In both sexes the earliest appearance of scent glands occurred in animals removed from their parents at weaning and reared in cages There was no difference between heterosexual pairs and mixed sex littermate groups (Experiment IV) If the parents were left in the cage scent gland development in their offspring was considerably delayed (Experiment II)

On the other hand the housing conditions were just as critical as the presence of the parents Thus littermate groups reared from weaning *in enclosures without parents* (Experiment III) showed an equal inhibition in scent gland development as those reared *in cages with parents* (Experiment II) Unfortunately no systematic record was kept for animals reared *in enclosures with parents* (Experiment I) but it was noted that when the glands were first examined all animals were over 20 wk old and not a single female out of 26 had a gland Some males

TABLE VII Experiment IV Fertility of Gerbils Placed in Cages at Weaning in Littermate Groups or Pairs

| | No of cages | Cages containing pregnant or parous ♀ (age 15–23 wk) | No of females | No of pregnant or parous ♀ (age 15–23 wk) | Age of birth of 1st litter (wk) |
|---|---|---|---|---|---|
| Groups | 7 | 6 | 25 | 11 | 15 |
| Pairs | 15 | 7 | 15 | 7 | 13 |

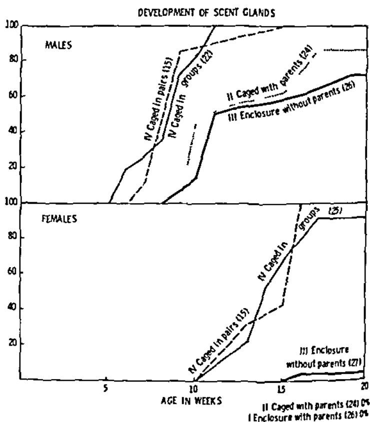



Fig 8 Age at development of scent glands in male and female gerbils under different rearing conditions.

had glands at this time but as it was not known when the glands had first appeared the data cannot be incorporated in this chart

It is obvious that the scent glands develop several weeks earlier in males than in females and that the degree of inhibition exerted by social factors is less severe in males Thus all males eventually had glands although these were often not actively secreting whereas many females did not have glands by the time they were almost a year old Other females developed glands which regressed following a change in the social structure

### Scent Gland Marking (Fig 9)

If the father was present his score was always the highest in the group None of the sons reared in enclosures marked during any of the tests Although 11 of 67 sons reared in cages showed some marking their mean score was less than half that of the fathers

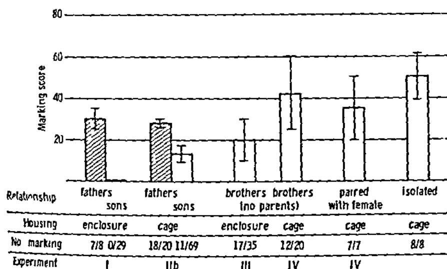



Fig 9 Scent gland marking scores of males reared under different social conditions

In littermate groups reared without parents about half the males marked The great variability in the marking scores of these animals is due to the fact that in each cage or enclosure there usually emerged one dominant male who marked considerably more than any of his brothers All males who had been paired with a single female from weaning showed high marking scores comparable to those of an additional group of males housed in individual cages

Marking scores of enclosure animals were generally lower than those of comparable cage animals which suggests that the enclosure environment had an inhibiting effect on this activity

Females marked much less than males The incidence of marking was greatest in isolated females and mothers living with their offspring

## DISCUSSION

Although the asymptotic population reached by freely breeding gerbil pairs was not much greater than that of hamsters living in similar enclosures (Goldman and Swanson 1975) the mechanism of control differed greatly In both species the founding mother bred repeatedly but in gerbils up to three litters survived whereas in hamsters never more than a single litter reached maturity The most

striking difference was in the fecundity of the daughters In hamsters all the daughters were fertile mated and were frequently pregnant but none of their pups lived beyond a few days of birth because they were cannibalized by conspecifics In contrast hardly any of the young female gerbils ever became pregnant in the presence of their parents and many showed signs of complete inhibition of sexual function

It was interesting that the asymptotic population was about the same (even higher) in gerbils confined to small cages as in those living in relatively spacious enclosures Although the absolute density was much greater in the cages the number of contacts between individuals was probably the same in view of the constant activity and gregarious nature of these rodents Even in the enclosures where there was a choice of nesting sites most animals chose to sleep together in one or two specific places Mothers with infants shared the communal nest without apparent detrimental effect on the young The gerbils in the crowded" cages all looked in good condition and reached similar size to those in enclosures When the population reached a certain absolute number newborn litters failed to survive and ultimately the mother usually ceased breeding

Lidicker (1965) observed that the asymptotic population reached by several species of rodents (house mouse rice rat deermouse and pinyon mouse) did not depend on the size of their enclosures He concluded that in a confined space it was not possible for the population to divide itself into more than one social grouping and hence limitations on the size of a single social unit was probably the proximate limiting factor This limitation certainly seems to apply to gerbils as Agren (1976) found that large (100 sq m) outdoor enclosures could not support more than one family unit Myers and Krebs (1974) mentioned that what is considered a high density in the field is a very low density indeed in the laboratory

Lidicker (1965) suggested that there was a correlation between the maximum size tolerated for a single social grouping and the causes of cessation of population growth The largest groups (28–34 individuals) were reached by the house mice and were associated with complete reproductive inhibition of females and partial inhibition of males The smallest grouping and lowest density (in rice rats) were associated with no decrease in natality but with high infant mortality Intermediate group sizes seen in deermice (14–29) were brought about by partial inhibition and some infant mortality Lidicker suggested that it is more efficient energetically to decrease natality than to go through the energy demanding process of reproduction only to have all the newborn killed He concluded that species like rice rats probably do not experience high densities in nature and hence have not evolved mechanisms for dealing efficiently with such conditions This would also seem to apply to hamsters (Goldman and Swanson 1975) On the other hand opportunistic species like house mice which can reach fairly high densities under favourable conditions have evolved a mechanism

for coping with such situations in an efficient manner A striking demonstration of this capacity was made by Crowcroft and Rowe (1958) In a colony of mice founded by two pairs complete regression of the reproductive tract occurred when the total population reached 150 this regression was reversed when the animals were dispersed into a much larger enclosures until a new asymptote was reached Family groups of deermice (Lidicker 1965 Terman 1965 1969) in confined conditions curb population growth by a combination of infant mortality cessation of reproduction by the mother and inhibition of daughters Gerbils seem to fall into the same category

The atrophy of sexual organs would seem to be due to inhibition of gonadotrophin secretion by social factors mediated through neural input to the hypothalamus The atrophic condition of the ovaries and uterus of the inhibited gerbils certainly supports this hypothesis

Several authors (Christian 1963 Brain 1971 Archer 1970) have suggested that gonadotrophin inhibition is secondary to an increase in ACTH produced in response to the stress of crowding Hull et al (1973 1976) found some evidence for this in colonies of gerbils kept under varying conditions of density Although the adrenals were weighed in some representative samples in the present experiment no consistent trends were seen But as the weight of the adrenals may not be a useful indication of their activity no conclusions can be drawn as to the role of the adrenals It can only be stated that in the most crowded cages all animals looked in excellent condition and did not superficially appear stressed

The social conditions which reversed reproductive inhibition of young females were pairing with males or removal of the mother In both situations the daughters were removed from their mother s influence but pairing was more conducive to litter survival Similar observations have been made in deermice (Sadleir 1965 Terman 1973a) as well as in hamsters (Goldman and Swanson 1965) The establishment of a new family unit by young adult pairs may be the natural method of dispersal Removal of the mother which may be analogous to death of the mother (eg by predation) in the wild was followed by conflict and fighting within the family as young females competed for top place in a hierarchy Several females usually conceived but few litters survived because of the social disruption Many females failed to become pregnant even though their reproductive tract was functional and still others remained inhibited It was impossible to determine which personality factors were responsible for the varying reactions of these females to the social situation

It is interesting to speculate as to the cues which led to reproductive inhibition in the presence of the mother – various modalities ie olfactory auditory general behaviour may be involved Experiments are in progress to determine which attributes of the mother are important ie being the genetic mother the rearing mother an older and larger female a breeding female or merely a fertile

*female* In this context it may be mentioned that removal of the other older larger parental animal ie the father had no effect on the female fecundity so long as the mother was still there conversely his continued presence after removal of the mother did not inhibit his daughters maturation

At this state it may be useful to consider the situation of young littermates growing up in the absence of both parents Young pairs living in cages matured and bred very early The age of first conception is in the range described in the literature (Norris and Adams 1974 Marston and Chang 1965) Littermate groups in cages also showed early sexual maturation and breeding (although few litters survived in the crowded conditions) and a remarkable lack of conflict In contrast littermates growing up in the much more spacious enclosures showed a delay in sexual maturation comparable to that seen when the parents were present At about 5 mo eventual sexual maturation was accompanied by fighting which culminated in the establishment of a breeding female (a situation reminiscent of removal of the mother) This may reflect the social structure in wild where towards the end of the season increasing conflict would lead to dispersal and establishment of new family groups Indeed such observations were made in the field on deermice (Sadleir 1965) and bank voles (Bujalska 1973)

The indiscriminate breeding – without apparent social structure – in the limited confines of a small cage supports numerous observations in mice that excessive crowding does not provide suitable conditions for the establishment of a social hierarchy (Calhoun 1973 Christian 1971) Hull et al (1973 1976) suggest that densely crowded gerbils showed a deficit in social reactivity when tested in paired encounters It is instructive to contrast the crowded cage situation with life in the enclosures in which the cohesiveness of the family group was illustrated by the animals cooperating in building a communal sleeping nest Frequent social contacts (ie sniffing chasing mock fights) were observed Following the birth of a litter the mother built a separate nest but after a few days she brought the infants to the communal nest where all members of the colony including the father participated in their care The initial transfer of the pups may be a protective mechanism as Elwood (1977) found that males and nonpregnant females cannibalized pups We have not seen any detrimental effect on litter survival attributable to the presence of the father as has been described by Ahroon and Fidura (1976)

The ventral scent gland in gerbils has been studied extensively Thiessen and his collaborators established that the gland appears around puberty and is larger in males than females It atrophies after gonadectomy and may be restored in either sex to the male size by testosterone and to the female size by estrogen and progesterone (Blum and Thiessen 1971 Nyby and Thiessen 1971 Owen and Thiessen 1973)

In the present experiment the ventral scent gland in the female gerbil provided a useful external index for assessment of reproductive status under varying

social conditions The absence of a gland in a chronologically adult animal was invariably associated with inhibition of the reproductive tract whether this was due to delayed puberty or secondary regression following a period of fecundity The ovaries were atrophic and contained only small follicles and no CL and the size and histological appearance of the uterus was comparable to that seen after ovariectomy

The small size of scent glands in sons compared to fathers and the positive correlation between scent gland and seminal vesicle weights suggest that also in males scent gland size may be used as an index of testosterone secretion This index is crude however since a relatively small amount of testosterone can restore the glands to normal and excess testosterone will cause no further growth (Thiessen Lindzey and Friend, 1968 Blum and Thiessen 1971) It is obvious that gonadotrophins in males were not suppressed to the same extent as in females by the presence of either parent The fertility of the young males was proved by their breeding record following pairing

Marking behaviour is also under the influence of testosterone although it is affected independently of the scent glands (Thiessen 1968 Lindzey et al 1968 Thiessen et al 1973 Yahr 1976) Scent gland development is limited by gland morphology so that it is impossible to produce "superglands" whereas one can produce supermarkers with excess testosterone (Thiessen Lindzey and Friend 1968 Blum and Thiessen 1971) The incidence of marking behaviour is strongly influenced by social conditions (Nyby et al 1970 Thiess n et al 1971 Yahr 1977) Thus it may be used as an index of dominance and as such it proved very useful in the present study Marking is elicited particularly in strange surroundings (Thiessen et al 1970 Baran and Glickman 1970) and the arena with pegs proved to be a powerful stimulus for marking in almost all fathers — many even continuing this activity when they returned to their home enclosures The suppression of marking in the sons therefore reflects a strong dominance subordinate relationship Marking increased in the sons after removal of the father but there was not sufficient time for a new hierarchy (and thereby a new high-marking male) to become established

Marking behaviour was so low in females living under colony conditions that it was not a useful measure of dominance (Yahr 1976) It has been reported that lactation increases marking (Wallace et al 1973 Yahr 1976) and as the mothers may have been lactating when they were tested this may account for their higher scores in comparison with daughters This phenomenon was not investigated systematically It is interesting that the mother exerted her influence on the daughters while the father s influence was primarily on the sons

Although the suppression of female fecundity and male marking by the parents may be viewed as an expression of parent-offspring conflict there was little overt aggression within the family The latent aggressiveness of these animals became apparent when a stranger was introduced into the colony one

that was almost always attacked Neither females nor juveniles were immune Such behaviour has been described by Thiessen and Dawber (1972) and Yahr (1977) and Wechkin and Cramer (1971) who concluded that the alien was attacked because he did not carry the community odour Ginsburg and Brand (1971) observed that even when tested in a clean cage former cagemates were not attacked while strangers were Attacks which were initiated by a resident lowered the threshold of aggression in the others so that indiscriminate fighting broke out Removal of the father stimulated a contest for dominance among the males while removal of the mother had a similar effect on the females Once again the lowered theshold of aggression also spread to animals of the opposite sex

An interesting perspective is given by Trivers in a theoretical paper entitled "Parent-Offspring Conflict (1974) in which he postulates that it is in the parents interest to promote altruistic behaviour among siblings (and thus suppress fighting) while it is in the offspring s interest to be selfish It is not in the parents interest to suppress aggression against strangers because they have no genetic investment in them Another aspect of the theory is that under certain conditions it is beneficial to the parents to suppress reproduction in the young – presumably when the number of animals that can be supported in a given environment is limited

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# Journal Review

MALEDICTA The International Journal of Verbal Aggression Maledicta Press 331 S Greenfield Avenue Waukesha Wisconsin 53186 Published 3–4 times yearly Individual subscription rates $10 00 yearly U S and Canada

I have just finished reading the first issue of Maledicta The International Journal of Verbal Aggression It is unique among scholarly journals a delight to read and almost impossible to put down Readers should be forewarned that they may find themselves overcome by an inexplicable urge to conceal Maledicta behind the covers of a more recognized journal — Science for example The impulse should be resisted at all costs however lest the reader have to explain to his colleagues what he finds so amusing about an issue of Science "

It is the stated editorial policy of Maledicta to publish any material sufficiently offensive to be rejected by the standard scholarly journals As such the journal specializes in research on and collections of verbal aggression pejoration derogation vituperation objurgation scurrility and the like Herein may lie the journal s biggest strength Stated simply Maledicta makes a wonderful thesaurus and the discriminating reader will never find himself wanting for choice of colorful expressions by which to convey his intimate feelings and moods to others

In addition to its role as a glossary the journal also functions as an outlet for more serious etymological literary psychological and cross-cultural investigations of maledictions For example the opening issue contains a piece on the use of sexual metaphors in the non Shakespearean drama of Renaissance England as well as an article on the origin of our strongest taboo word On the lighter side is a psychologically toned article reminiscent of Theophrastus s character sketches Its title How to judge people s character by their farting styles

In brief Maledicta contains a potpourri of sayings articles odes and poems devoted to the discussion and expression of obscenity There is a little something for everyone And all in all the journal provides a welcome respite from the tedium often produced by more typical academic annals

Michael F Scheier

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AGGRESSIVE BEHAVIOR
Volume 4 pages 93–103

# A Guide to the Literature on Aggressive Behavior

Articles relating to the general problem area of aggression are scattered throughout the whole range of specialized journals in fields from A for anatomy to Z for Zoology It is virtually impossible for a single individual to find all the articles which may bear on his particular interest Information overload is of course a problem However an even greater problem is matching the interesting article with the interested reader Aggressive Behavior will attempt to alleviate this problem by publishing a list of references in each issue The reference list will be compiled from several sources Each article listed in Psychological Abstracts and indexed under the following terms will be included

1 Aggressive Behavior
2 Anger
3 Animal Aggressive Behavior
4 Attack Behavior
5 Hostility
6 Threat Postures
7 Violence
8 Frustration
9 Conflict

Each reference will be coded according to the index terms listed above and will be listed in alphabetical order by senior author There are a large number of journals that publish articles related to aggression that are not covered by Psychological Abstracts In order to find such references the cooperation of all readers of this journal is needed If each of the several hundred investigators concerned with the problem of aggression makes a habit of contributing to the literature search section of Aggressive Behavior the search task of each of us will be made easier If in your coverage of the literature you find an article about aggression in a journal that is not regularly abstracted by Psychological Abstracts put the full reference on a 3 X 5 card and send it to the editor for inclusion in this section

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AGGRESSIVE BEHAVIOR
Volume 4 pages 105–113

# ailure to Induce Aggression in ihibited and in Genetically on-Aggressive Mice Through ijections of Ethyl Alcohol

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Two kinds of nonaggressive mice were used as subjects 1) males from a strain selectively bred for nonaggressiveness (TNA) and 2) males from a strain selectively bred for aggressiveness (TA) but made nonaggressive by defeats in fights. The aggressiveness of neither type of animal was increased by injections of ethyl alcohol in concentrations of 1 gm/kg and 1 5 gm/kg Three series of experiments were performed. The results were incompatible with the assumption of a general physiological aggression-heightening effect of ethanol and also with an assumption of removal by alcohol of learned inhibitions against aggression.

y words aggression, alcohol, inhibited aggression, genetic nonaggression

## NTRODUCTION

In humans considerable evidence links alcohol to increased violence [eg inklenberg 1973] and alcohol has been assumed to have a general aggression eightening effect [Taylor and Gammon 1970] although some laboratory ex eriments with humans show contrary evidence [Bennett et al 1969 Lang et al 975]

There is surprisingly little information on the effect of ethanol on aggressive ehavior in animals Raynes et al [1968] reported increased aggressive behavior n Siamese fighting fish (Betta splendens) under the influence of alcohol On the

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other hand Crowley et al [1974] found no measurable effect on submission or dominance behavior in monkeys

On the psychological level the assumed aggression heightening effect of alcohol has been explained by two types of theory [Bennett et al 1969] 1) The first disinhibition postulates that alcohol lowers the inhibitions against aggression which the individual has acquired through learning This theory has to some extent been substantiated by the results showing that alcohol can diminish fear and anxiety reactions in animals [Kaplan 1955 Scarborough 1957 Pohorecky et al 1976] 2) The second theory suggests that alcohol enhances aggression directly ie through some mechanism other than disinhibition

The three experiments of the present study were originally designed to decide between these two hypotheses Nonaggressive mice can be obtained by principally two different means by selective breeding and by punishment of aggression [Lagerspetz 1964] The former produces animals that are genotypical nonaggressive The latter provides phenotypically nonaggressive animals or animals with learned inhibitions against aggression

We used the animals from the two mouse strains selectively bred for aggressiveness (TA Turku Aggressive) and nonaggressiveness (TNA Turku Non aggressive) for 26 generations by the senior author (Lagerspetz 1961 1964 Lagerspetz and Lagerspetz 1971] The animals of the TA strain are highly aggressive but can by successive severe defeats in fights be made temporarily nonagressive Most of the TNA animals do not show any aggression even though reared in isolation Through training they can be made to show only a slight degree of aggression The effects of training on the aggression level of TA and TNA mice are described in the above mentioned articles by Lagerspetz

The purpose of the three series of experiments described here was to find out if the presence of alcohol affects differently the two types of nonaggressive animals mice of a genetically nonaggressive strain and mice of a genetically aggressive strain whose aggression has been inhibited by defeats If alcohol has a nonspecific aggression-enhancing effect the aggressiveness of both types of animals would be expected to increase On the other hand if the possible aggression heightening effect of alcohol depends on the lessening of learned inhibitions against aggression the aggression level of TA animals trained to nonaggression would increase whereas the aggressiveness of the genetically nonaggressive TNA animals which have had no punishment of aggressive reactions would remain unaltered under the influence of alcohol

## EXPERIMENT 1

### Method

Subjects Of the subjects 42 animals were males from TA strain of these 22 were from the 17th generation selectively bred for aggressiveness (TA $S_{17}$

age 6 months at the start of the experiment these are called old animals) and 20 were derived from TA $S_{18}$ (young animals age 2 months) Fifteen males of the TNA strain were used of which five came from the 17th generation of selection for nonaggression $S_{17}$ and ten from $S_{18}$ Mice of the TNA strain which had become somewhat aggressive in isolation (see below) were excluded

All animals had been reared alone in their separate cages since weaning This is the standard way in our laboratory to keep animals that will be used in tests of social behavior The purpose of this procedure is to ensure that the variation of aggressiveness of the animals depends on genetic factors and not on social learning which has been found to change the aggression level of the animals of these strains [Lagerspetz 1964] The weight of the old animals was 25–31 gm and that of the young ones was 22–26 gm

Before the start of the experiment all animals were tested for aggression in four successive trials The TA animals were divided into two groups matched on basis of their scores in the aggression tests and their age Because of the small number of the TNA animals these were used as their own controls

*Training to nonaggression* All the animals of the aggressive strain were trained to nonaggression by encounters with aggressive opponents for four minutes The method of training has been described previously by Lagerspetz [1961 1964] As opponents TA mice from $S_{17}$ known to be highly aggressive were used (not included in the experimental groups)

Immediately before starting the training trials they were stimulated to aggression by a bottle brush [see Lagerspetz and Mettälä 1965] If the experimental subject won the bout the opponent was replaced by a fresh one so that the training trial lasted four minutes altogether However if the opponent bit the subject hard enough to draw blood the trial was discontinued This was done in order to provide approximately the same amount of punishment to all the animals of the experimental group eg to avoid overlearning of nonaggression Each TA animal was defeated on eight successive days once a day On the basis of previous experiments [Lagerspetz 1964 p 61] this was considered a suitable amount of training to obtain nonaggression in TA males The TNA mice were not given any training before the alcohol and control experiments

Thereafter the experimental TA subjects were tested after having received alcohol and the control TA animals after NaCl injections The TNA mice received both alcohol and NaCl injections (see below)

*Measurement of aggression* To test the aggression of a subject a standard opponent was put into its cage and the behavior of the subject was recorded during seven minutes The use of standard opponents has previously been described by Lagerspetz [1964] The opponents were mice from a Swiss albino strain from which the two selectively bred strains had originally been derived The opponent animals had been reared in colonies and previously tested for not behaving aggressively They never showed any signs of aggression during the encounters

The most important indicators of mouse aggression are biting and tail rattling [Mettala 1965] The occurrence of biting and bouts of tail rattling during each minute were recorded The sums of occurrence in seven minutes were used as the aggression scores of the animals

The testing of aggression was started 15 minutes after the injection of alcohol or NaCl (see below) The injections were given and the aggression of the TA animals was tested three times at intervals of one day The TNA animals serving as their own controls were injected and tested six times altogether the trials with alcohol and control fluid were alternated The significances of the differences between the groups and the treatments were tested with Student s t test

Injections of alcohol and control fluid Alcohol was injected intraperitoneally in a concentration of 1 gm/kg as a 10% solution As control fluid 0 9% NaCl was used it was injected in an amount comparable to the alcohol solution in proportion to the body weight of the animal The alcohol dosage was chosen because it was considered high enough to have an effect but not so high as to impair the motor activity of the animals [Arvola 1960] In fact doses of 1–2 gm/kg increase the motor activity of mice [Arvola 1960 Lagerspetz 1972]

## Results

Table I shows the means of biting and tail rattling of the three seven minute test trials after alcohol or control injections The results of the old and young animals were so similar that it was considered justified to treat them together It will be recalled that the figures for the inhibited TA animals are results of two groups experimental and control whereas those of the TNA animals are derived from retests of the same animals

The biting and tail rattling frequencies of the TA animals are still after completion of training to nonaggression higher than those of the TNA animals. This reflects the fact that the training should have been more severe

**TABLE I** Biting and Tail Rattling in Animals of the Inhibited Aggressive TA Groups (N = 21 + 21) and in the Genetically Nonaggressive TNA group (N = 15)*

| | TA inhibited | | TNA | |
|---|---|---|---|---|
| | Biting | Tail rattling | Biting | Tail rattling |
| Before experiments | 15 57[a] | 36 51[a] | 1 82 | 2 30 |
| Alcohol | 5 81 | 5 36 | 1 67 | 1 40 |
| NaCl | 2 54 | 3 02 | 1 73 | 1 67 |

*Mean during seven minutes The TNA animals served as their own controls Significances of differences are given in the text
[a]N = 42

The alcohol injections had no effect on the aggressiveness of the TNA mice In the TA animals the group that received alcohol injections showed a slightly higher level of aggression than the control group Although this difference did not reach the level of statistical significance we decided to continue the experiments on the effect of alcohol on inhibited aggression

## EXPERIMENT 2

### Method

Subjects Since the purpose of this experiment was to investigate only the effect of alcohol on aggression in originally aggressive animals the aggression of which has been inhibited by defeats only TA mice were used as subjects These were 16 males from $S_{21}$ aged 10–11 months They weighed 25–31 gm and had been reared in isolation since weaning The animals were assigned to two groups experimental and control by matching on basis of their performance in the training trials (see below) both the rapidity of learning and the starting level of aggressiveness were taken into account

Training to nonaggression The aggression tests with standard opponents and the training to nonaggression through defeats were carried out in a similar way as in Experiment 1 However in order to know when the criterion of no biting or tail rattling was reached and to avoid overlearning the subjects were tested with a standard partner after every third training trial If the subject did not show any aggression the defeats were discontinued after three additional training trials In this way the animals got different numbers of trials 15 trials being the highest and 6 the lowest but hopefully a comparable amount of inhibition

Injections of alcohol and control fluid The animals were injected with two doses of 10% ethanol 1 0 gm/kg and 1 5 gm/kg The animals of the experimental group (N = 8) were injected four times with both alcohol dosages in a counter balanced order [Underwood 1949 pp 323–327] The control animals got comparable amounts of 0 9% NaCl The injections were given at intervals of two to four days

At the beginning of the experimental series the aggression of the animals was tested both 20 and 50 minutes after they had received the injection It became clear however that the greater effects of alcohol could be observed 20 minutes after the injection whereas after 50 minutes the behavior was nearer to normal Accordingly the results are calculated on basis of records taken 20 minutes after the injection

Testing of aggression Aggression was measured in a similar way as in Experiment 1 In addition to the tests made in connection with the alcohol and control injections the aggression of all subjects was tested between these experimental trials in order to record the general level of aggression during the same time

period when the experiments were carried out These were never carried out on the same day as the experimental trials These trials are called Normal tests Each animal participated in Normal tests eight times

## Results

Table II shows that the alcohol group again showed somewhat more aggression than the control group as reflected in the biting frequencies Calculated by the Wilcoxon matched pairs signed rank test [Siegel 1956] only the following differences were significant the difference in bite frequencies between the alcohol (1.5 gm/kg) and NaCl group (4% level) the difference in tail rattling between the two alcohol dosages (2% level) and the difference in biting between Normal tests and NaCl group (1%) The measures taken before the start of the punishment training differ highly significantly from all the corresponding measures after training

When the normal tests made between the injection experiments are taken into account the significance of alcohol is far from clear At least one can conclude that alcohol does not restore the level of aggressive behavior the animals had before the inhibition training

## EXPERIMENT 3

The purpose of this experiment was to test the original hypothesis of Experiment 1 once more but the larger groups of animals and with a sufficiently severe training to nonaggression It will be recalled that in Experiment 1 the training to nonaggression was not complete

## Method

The subjects were 24 males from the TA and 34 males from the TNA strain both derived from $S_{22}$ The age of the animals was 6–7 months and their weight was 22–36 gm All TA mice were trained to nonaggression in a similar way as in

TABLE II Biting and Tail Rattling of Inhibited TA Animals*

| | Biting | Tail rattling |
|---|---|---|
| Before training (N = 16) | 17 80 | 37 25 |
| Normal tests (N = 16) | 3 70 | 12 40 |
| NaCl (N = 8) | 1 90 | 14 82 |
| Alcohol (1 0 gm/kg) (N = 8) | 2 33 | 16 20 |
| Alcohol (1 5 gm/kg) (N = 8) | 2 52 | 9 40 |

*Mean during seven minutes Significances of the differences are given in the text

Experiments 1 and 2 As trainer animals those ten males from TA $S_{22}$ that had proven the most aggressive in an initial aggression test were chosen

Due to the high aggression of the trainers and also to the lower aggression of the trainees at the start of the training the aggression of the TA males was inhibited more quickly than in Experiment 2 After three training trials no ubjects showed biting or tail rattling whereafter they were given three additional training trials This was the same procedure as in Experiment 2 The more effective inhibition of aggression of the TA animals in this experiment can also be due to the fact that the trainees in this experiment were younger than those of Experiment 2 and the aggressiveness of mice increases with age [Lagerspetz and Mettala Portin 1968] Again the TNA animals received no training

The animals were not divided into an experimental and control group but all animals were tested in all conditions being assigned to these in different orders

Two alcohol dosages were again used 1 0 and 1 5 gm/kg Each animal was injected four times with alcohol twice with each dosage and four times with NaCl The aggressiveness was tested 20 minutes after the injection in the same way as previously In addition the animals were tested between the trials in Normal tests as in Experiment 2

### Results

At the beginning of the experiments after the training of TA animals had been completed the aggression level of all animals was very low Differences from zero aggression were too few to justify statistical treatment of the frequencies of occurrence of tail rattling and biting

Table III shows that the level of aggression of the TA animals which had been trained down to 0 0 in both biting and tail rattling did not rise under the influence of alcohol On the contrary some aggression is shown in the Normal tests and after the control injections by TNA animals It can be concluded that the results of Experiment 3 did not show any aggression increasing effect whatsoever of alcohol

## DISCUSSION

The results did not give support to either of the two hypotheses presented in the introduction Alcohol did not in a general way increase the level of aggression of the animals nor did it specifically remove or diminish the inhibitions of aggression which were acquired through learning

When trying to find explanations for increase of violence in humans under the influence of alcohol if there is no evidence of an increase of aggression in lower mammals direct pharmacological and physiological causation can be ruled out and the causes have to be sought on a more complicated psychological level If

TABLE III Biting and Tail Rattling in the Inhibited TA Animals (N = 24) and in the Genetically Nonaggressive TNA Animals (N = 34) *

| | TA inhibited | | TNA | |
|---|---|---|---|---|
| | Biting | Tail rattling | Biting | Tail rattling |
| Before experiments | 5 51 | 35 30 | 0 00 | 0 00 |
| After training | 0 00 | 0 00 | – | – |
| Normal tests | 0 04 | 0 25 | 0 03 | 0 15 |
| NaCl | 0 00 | 0 05 | 0 10 | 0 15 |
| Alcohol (1 0 gm/kg) | 0 00 | 0 00 | 0 02 | 0 09 |
| Alcohol (1 5 gm/kg) | 0 00 | 0 06 | 0 00 | 0 03 |

*Mean during seven minutes

alcohol had a very clear-cut pharmacological aggression-enhancing or inhibition diminishing effect it would certainly be observed even in lower mammals

Raynes et al [1968] observed an increase of aggressive behavior in the Siamese fighting fish under the influence of alcohol However since the alcohol was administered by immersing the fish into an alcohol solution the peripheral influence of alcohol as a noxious stimulus cannot be ruled out This might make the results not directly comparable to experiments in which alcohol is administered orally intraperitoneally or intravenously

In the literature on the effects of alcohol the relationship between aggression and alcohol is often touched upon but seldom directly investigated It may be that attempts to investigate it have often resulted in failure to find a relationship as was the case in the present study

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AGGRESSIVE BEHAVIOR
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# Level of Instigation and Model Similarity as Determinants of Aggressive Behavior

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A study was conducted to replicate and extend a finding by Wheeler and Levine [1967] indicating that a dissimilar model was more effective in inducing the contagion of aggression than a similar model On the basis of recent findings suggesting the circumstances under which dissimilar others are more influential than similar others, the following predictions were derived When subjects are highly instigated dissimilar models can influence subjects to be more aggressive than can similar models when subjects are under a low degree of instigation similar models will influence subjects to be more aggressive Subjects presented their point of view on a case study in a three-person group discussion setting Then subjects heard the second person (instigator) attack their position in a highly abusive or slightly abusive manner (High vs Low Instigation) Next subjects heard a third person whom they had been led to believe was similar or dissimilar to themselves, attack the instigator (Similar vs Dissimilar Model) Finally subjects had an opportunity to express their feelings to the instigator The results supported the predictions.

Key words model similarity instigation aggressive behavior

## INTRODUCTION

Several recent studies have indicated that aggressive models can affect the magnitude of subsequent aggressive behavior from observers [Bandura Ross and Ross 1961] Some of these investigations have considered the characteristics of the model to be an important determinant of the extent to which the observer

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follows the model s behavior [Baron and Kepner 1970] A study of verbal aggression by Wheeler and Levine [1967] obtained a somewhat counterintuitive finding in this area Opposite from what was predicted they found that a dissimilar model was more effective in inducing the contagion of aggression than a similar model A study of physical aggression by Baron and Kepner [1970] reported a somewhat similar finding Baron and Kepner explored the relation between attraction to an aggressive model and subjects aggressive behavior Attraction was manipulated *through attitude similarity and it was found* using one measure of aggression (duration of shock) that aggression increased over time when the aggressive model was dissimilar but not when he was similar In both studies opposite effects were predicted The purpose of the present study is to explore the determinants of verbal aggression using a procedure similar to the one used by Wheeler and Levine and specifically to explore further the role of model similarity as a determinant of aggression

While Wheeler and Levine were uncertain as to the explanation of their findings the results seem to fit nicely with some recent research on the triangulation effect [Goethals and Nelson 1973] S udies by Goethals [1972] and Goethals and Nelson [1973] have shown that under some circumstances the agreement of a dissimilar other is more impressive and influential than the agreement of a similar other This phenomenon is understandable in terms of Kelley s [1967] attribution theory and has been called triangulation If an individual finds that a dissimilar other makes the same judgment about an entity that he does he can be more confident that his judgement is an accurate reflection of the entity rather than a biased person caused response The agreement of a similar other may be caused by the same biasing characteristics and is thus less impressive The explanation of the Wheeler and Levine findings in terms of triangulation views the behavior of the aggressive model as an indication of agreement with the subjects.

To make this clearer it can be recalled that in the Wheeler and Levine experiment naval recruits listened to two of their peers expound on several topics of current political and social interest The first person the instigator took extremely socially undesirable positions in a fairly obnoxious manner The second person the model attacked the first when his turn came to speak Finally the subject had a chance to speak and Wheeler and Levine measured the extent to which the subject followed the model s lead in being verbally agressive toward the instigator A critical feature it will be argued is that the level of instigation in this procedure was quite high [Wheeler personal communication] Incidentally the level of instigation was also very high in the Baron and Kepner procedure

If the subject is highly instigated to aggress and then observes another person similarly instigated modeling aggressive behavior the model s behavior can be considered an instance of agreement as to the appropriate way of responding to the instigator Since the subject may well be uncertain as to the appropriateness of aggression the situation is perfectly structured for obtaining a triangulation

effect The aggression of the dissimilar model helps the subject rule out the possibility that his view of the situation as one where some aggressiveness is called for is simply a reflection of personal bias or idiosyncrasy The modeling of the similar model is less helpful in this regard

More generally it can be added that the logic of triangulation may be particularly salient in situations such as this where subjects are making judgments about the appropriateness of behaviors which are relatively low in social desirability It is when people are making decisions about such behavior that they might be sensitive to the fact that they can act inappropriately because of their own personal biases needs or idiosyncrasies Then support from dissimilar others would provide highly desired evidence that their judgments and wishes are appropriate and widely shared Support from similar others precisely because they are similar in possible biasing characteristics simply would not be as influential

Returning to the aggressive modeling situation the importance of the level of instigation is that the model s aggression can only be conceived of as an instance of agreement with the subject s view of the situation when instigation is high If instigation is fairly low aggressive behavior from the model may seem inappropriate It may disagree with the subject s view of the situation and his judgment as to the appropriate response Under these circumstances would a similar or dissimilar model be more effective? The Goethals [1972] study concurs with the thrust of other social influence literature in showing that when another person disagrees he is more influential when he is similar than when he is dissimilar

Thus we are led to the specific predictions of the study Under conditions of high instigation an aggressive model may be implicitly agreeing with the subject as to the appropriate behavior toward the instigator Here triangulation would come into play and it is predicted that the Wheeler and Levine finding will be replicated The dissimilar model will induce more aggression from the subject than the similar model Under conditions of low instigation where the model s behavior may constitute implicit disagreement he should be more influential and induce more aggression if he is similar This predicted interaction was tested in a 2 (High vs Low Instigation) X 2 (Similar vs Dissimilar Model) factorial experiment modeled closely after that of Wheeler and Levine

## METHOD

### Overview

Subjects reported individually for an experiment described as a study of group discussion They were taken to a cubicle equipped with a speaker and microphone and told that two other subjects were in similar adjoining cubicles Subjects were told that there would be an exchange of special interests forms describing their interests and activities in order to allow participants to know something about

each other Each subject always designated A received forms from the others designated B and C B s form was always the same and typical for the subjects population The form for C was completed along prepared guidelines to give the impression that C was either very similar or very dissimilar to the subject in his interests and tastes

A discussion procedure was explained in which the participants read the case history of a delinquent boy and presented their views of the most effective treatment for him over an intercom system After the subject spoke he heard one of two prerecorded tapes representing B In the High Instigation condition B took a highly socially undesirable position aggressing strongly and personalistically against A In the Low Instigation condition the tape took a milder position aggressing only slightly and apologizing frequently Then the tape for C was heard It contained a strong attack against B The subjects were than asked to speak again The degree of verbal aggression expressed against B was the major dependent variable

## Subjects

The 35 subjects were male residents of Williamstown Mass ages 18–20 Subjects were contacted and scheduled by telephone at their homes They were randomly assigned to one of the four experimental conditions with the constraint that the numbers of subjects in each condition be as close to equal as possible

## Procedure

When the subject arrived the experimenter led him to a vestibule where there were three rooms conspicuously labeled Discussion Room A B or C and a fourth room labeled Experimental Control Room The subject was seated in Room A given the code name Subject A and told that the focus of the research was the dynamics of group discussion The experimenter stated that a new format a controlled anonymous group discussion had been devised in order to eliminate problems such as unequal speaking terms of participants uncontrolled nonverbal communication reluctance to speak frankly etc He explained that there were two other people in the discussion both students from the local area of their age but they would not see the others or learn their names He added that a speaking order (A B C A) had been determined which would allow A the subject to go last so as to compensate for the disadvantages of going first The experimenter emphasized that he hoped the anonymous procedure would encourage openness and frankness in the discussion

At this point subjects were given two copies of a special interests form" which asked them to list their favorite topics in school favorite activities magazines movies music etc The experimenter explained that an exchange of such forms could loosen things up and give them some idea of the kinds of persons in the discussion Then the experimenter explained that subject B had arrived a

bit earlier and was already completing the forms and that he had better leave the subject to greet the third person He added that he would return with B s and C's forms

The experimenter returned several minutes later collected the subject s completed forms gave him one allegedly from B and left saying he would return with C's form When the experimenter left the room he took the subject s form and prepared a bogus form for C which was designed to be highly similar or highly dissimilar to the subject s The procedures for completing C s forms were detailed in advance The number of identical similar or dissimilar answers to be used on each section of the form were specified with instructions for dealing with specific common responses When the form for C was completed the experimenter returned and looked over the subject s shoulder arranged the forms for B and C and asked to examine them for a moment He remarked that B s form was not too similar or different from the subjects and then asked to look at C s After a long pause the experimenter said in the Similar condition Hmmm It s very unusual to find two forms so close in one discussion group He pointed to similar or identical responses and added I get the feeling that you two are pretty similar In the Dissimilar condition he said Hmmm It s very unusual to find two forms so distant in one discussion group You have almost no same or even similar items you really don t seem to have much in common with C In both conditions subjects often spontaneously noted their similarity or dissimilarity to C during the experimenter s pause

Then the experimenter asked the subjects to complete a form labeled Personal Impressions Questionnaire He explained that the purpose of the form was to assess first impressions which might affect the discussion The forms asked the subject how similar he felt to B and C and to what extent he felt he could become good friends with them

At this point the discussion procedures were explained All instructions were given over the intercom system from the control room First the subjects were told to read the case history (actually fictitious) of Bobby James a black teenager from Harlem who was often in trouble with the police The case itself and an accompanying seven point Kindness Punishment Scale were modeled closely after the Johnny Rocco materials used in Schachter s [1951] experiment After the subjects had read the case they were told to consider the Kindness Punishment Scale and the seven alternative treatments for helping Bobby James Then they were asked to indicate on a form their choice from the scale and their confidence that it was the correct choice At this point the experimenter answered any questions and started the actual discussion He emphasized that all participants should be as frank and direct as possible in expressing themselves The experimenter instructed A (the subject) to present first his position regarding Bobby James He was asked to give his treatment recommendation his confidence and his reasons for that choice He asked B and C to listen to A carefully so that they

could respond to him when their turn came A was given 30 seconds to organize his thoughts and then was asked to speak

After the subject spoke the experimenter thanked him and asked B to speak. At this point the experimenter started a tape recording which represented B Bs tapes had been prepared on the basis of the assumption that all subjects would take a position toward the kindness end of the Kindness Punishment Scale (This assumption proved to be correct ) Accordingly B s speech was a critique of the softness and naivete of A s recommendation for helping Bobby James without stressing discipline B s attack was severely abusive and personalistic in the High Instigation condition B characterized the subjects thinking and integrity in extremely hostile terms and in a bitterly sarcastic tone of voice In the Low Instigation condition B also attacked the subjects position but in a very different way His tone was mild and he apologized for his disagreement saying he simply had to make his differences known

When B s tape had finished the experimenter thanked B and told C to prepare his position Then C s speech was played It was a strong attack on B It was designed to be more abusive than B s Low Instigation tape but less abusive than B s High Instigation tape The tape concluded by saying that he C agreed pretty much with A and that he hoped A could do a better job of answering B than he did This final comment was included to give the subject more of an invitation than he already had to speak aggressively to B Finally the experimenter thanked C and said that A would now have the final speaking turn

When the subject had finished his second turn the experimenter thanked all the participants and said he would come around to have them complete some final questionnaires These forms included questionnaires asking the subject to indicate his impression of both B and C on bipolar nine point scales with the following items Influential not influential intelligent not intelligent hostile not hostile open minded closed minded likeable unlikeable sensitive insensitive helpful not helpful When the subject had completed the forms the experimenter debriefed him thoroughly

## RESULTS

Four subjects revealed during the debriefing that they were suspicious of the procedures employed in the experiment In all cases these suspicions concerned the authenticity of the statements they heard from B and C The data from these four subjects were eliminated from the analysis

### Validation of the Manipulations

The subjects were asked to indicate the degree to which they felt similar or dissimilar to C An analysis of variance performed on these data revealed only a main effect for similarity Subjects in the Similar conditions felt more similar to

C than did subjects in the Dissimilar conditions (F = 29 10 1 and 27 df p < 0 001) The attempt to manipulate the subjects perceptions of their similarity to C was apparently successful

A check on the level of instigation manipulation was contained on the final "personal impressions questionnaire where subjects were asked to rate B and C along several dimensions including hostility (1–9 point scale) An analysis of variance of these ratings revealed only a main effect for Instigation (F = 5 74 1 and 27 df p < 0 05) It seems that our effort to manipulate the subjects perceptions of B s level of instigation was successful It can be noted however that even in the Low Instigation conditions the mean rating of B s hostility was slightly over the midpoint of the scale

## Aggression Towards B

The subjects final statements were rated for the extent to which they expressed aggression toward B There were two raters who were unfamiliar with the hypotheses of the study The raters used the four categories of aggression used in the Wheeler and Levine [1967] study (0 = none 1 = slight 2 = moderate 3 = extreme) The raters gave identical scores in 81% of the cases The correlation between the two sets of ratings was r = 0 93 In all cases of disagreement the difference in ratings was only one category Since the ratings were so closely correlated it was decided to simply average the two raters scores and conduct an analysis on the average scores The analysis is identical if the scores of the two raters are analyzed separately

The means of the average ratings are presented in Table I An analysis of variance performed on these data reveals the predicted interaction between Similarity and Instigation (F = 7 05 1 and 27 df p < 0 02) Planned comparisons also revealed that within the High Instigation conditions there is more aggression expressed toward B when the Model C is dissimilar (t = 2 17 27 df p < 0 05) Within Low Instigation conditions there is as predicted more aggression directed toward B when C is similar than when C is dissimilar but the difference does not reach significance (t = 1 60 27 df p < 0 15) The overall analysis of variance also revealed a trend toward a main effect for instigation (F = 2 51 1 and 27 df p < 0 15) There tended to be slightly more aggression under High Instigation conditions

## Other Findings

Additional analyses of subjects impressions of B and C revealed very little of further interest Subjects impressions of B were significantly more negative in High than in Low Instigation It had been expected that subjects impressions of the model (C) might be more negative under Low Instigation conditions In that situation his own abusiveness toward the instigator may seem somewhat inappropriate There is no evidence to support this presiction Relative to subjects impressions of B their impressions of C were uniformly positive in all con

**TABLE I Mean Ratings of Subjects Aggression Toward B**

| | Similar | Dissimilar |
|---|---|---|
| High instigation | 0 50 (n = 9) | 1 57 (n = 7) |
| Low instigation | 0 88 (n = 8) | 0 07 (n = 7) |

ditions and on all measures There was however one finding of interest The model was seen as significantly more open minded ($F = 5\ 13$ 1 and 27 df $p < 0\ 05$) when he was dissimilar than when he was similar This finding is probably due to the fact that his agreement with the subject regarding the case study was probably less expected when he was dissimilar It may indicate that the dissimilar model has high credibility (although he is not rated as more influential ) resulting in his ability to triangulate the subjects desire to aggress in the High Instigation condition

## DISCUSSION

The results of the study give support to the predicted interactive effects of level of instigation and model similarity on aggressive behavior When the level of instigation was high the Wheeler and Levine [1967] findings were clearly replicated There was more aggression when the model was dissimilar than when he was similar When the level of instigation was low there was a nonsignificant trend in the opposite direction The difference between differences was substantial enough to yield a significant interaction

Although the predicted interaction was obtained the data are odd in one respect The average level of aggressive behavior is actually higher in the Low Similar than in the High Similar condition Although this difference does not approach significance ($t < 1$) any difference between the two conditions might be expected to be in the opposite direction Why should the level of aggression be so low in the High Instigation Similar Model condition?

During debriefing High Instigation subjects commented that they were quite angry and since the situation was rather highly charged they were careful about what they said They wanted to be even more careful about speaking harshly than they ordinarily were and only felt comfortable in expressing their anger and hostility when they had really good evidence that such expression was appropriate Subjects in the High Dissimilar condition felt that they had such evidence When the dissimilar model was aggressive they felt sure that it was appropriate

to be hostile toward the instigator and several of them were quite so Subjects in the High Similar conditions indicated that they expected the model to be angry as they were and perhaps to be aggressive but they could not really be sure it was appropriate Only the rather unexpected support from dissimilar models seems to have been effective in releasing angry subjects from constraints on their verbal behaviors which may have been more severe than usual

One of the clearer aspects of the present data is that the dissimilar model elicits more aggression from subjects than the similar model under High Instigation conditions It is important to note that this effect has now been found twice in investigations of verbal aggression and once in a study of physical aggression [Baron and Kepner 1970] Although there seems to be some justification for regarding the finding as reliable the matter of explanation is more difficult The present study was designed to support an explanation based on the attributional concept of triangulation However the obtained pattern of results suggest an alternative although not altogether different explanation that focuses on communicator credibility It will be recalled that the data from one of the secondary measures showed that the dissimilar model was perceived to be more open minded than the similar model probably because of his unexpected agreement with the subjects This finding suggests that the dissimilar model was overall more credible than the similar model It can be argued further that any difference in credibility favoring one model or the other would only be important in the high instigation conditions Only in the high instigation conditions are subjects uncertain about the appropriate behavior Under these conditions of uncertainty they should be relatively open to the influence of a credible model In the low instigation conditions on the other hand the subjects probably feel relaxed and would not be receptive to an influence attempt toward aggression Here any difference in the credibility of the models should be of relatively little importance This analysis closely parallels Brock s [1964] theory of persuasion which proposes influence to be a multiplicative function of credibility and receptivity [Osterhouse and Brock 1965]

Regarding the dissimilar model as more credible because of his unexpected agreement is close to the logic of triangulation whereby subjects are more confident due to the unexpected agreement of a dissimilar other that their own judgment rests on a broad consensus but it is not identical The triangulation idea proposes a concern about personal bias and about consensus in formation that are not part of the credibility argument There is no direct evidence that subjects are concerned with these questions and choosing between the two explanations for the results is difficult The attribution triangulation analysis predicts an interaction where the similar model is more influential than the dissimilar model in low instigation conditions The credibility X receptivity analysis predicts an interaction whereby there is little difference in influence produced by the

similar and dissimilar models in the low instigation conditions although any difference should be in the direction of greater influence for the dissimilar model The data suggest that the similar model is more influential than the dissimilar model in the low instigation conditions but the difference is not significant The results seem slightly more in accord with the attributional analysis but not unequivocally so It seems clear that more research is needed

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AGGRESSIVE BEHAVIOR
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# Alcohol and the Prior Residence Effect in Male Convict Cichlids (Cichlasoma nigrofasciatum)

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A series of experiments were undertaken to demonstrate the dominance advantage of a territorial resident over an intruder (the prior residence effect) in the adult male Convict Cichlid (Cichlasoma nigrofasciatum) and to evaluate the effects of alcohol (ethanol) on this phenomenon After successfully demonstrating the prior residence effect additional experiments were conducted in which the resident or intruder was given one of three different doses of ethanol (0.15% 0 20% 0 35%) These doses have previously been shown to reduce or increase intraspecific aggression in this species. Over the entire dosage range, drugging the intruder produced no changes in the dominance advantage of the resident. However drugging the resident at the higher doses (0 20% 0 35%) resulted in loss of the resident s dominance advantage These effects were not due to impaired locomotor behavior of the drugged fish as no abnormal motor behaviors were noted In general as reported in previous studies, the resident fish, whether drugged or not typically attacked first Also as has been previously shown the fish that attacked (bit) first typically showed eventual dominance. The present results show that the dominance advantage of the territorial resident is not altered by giving an intruder a hypo- or hyperaggression-producing dose of alcohol. Changes in the dominance advantage occur only as a function of drugging the resident thereby providing evidence that the behavior of the territorial resident is either directly or indirectly (reaction of the intruder to these changes) responsible for the prior residence effect. The present studies also provide some pharmacological approaches for determining the variables important in a laboratory analog of a naturally occurring instance of intraspecific aggression.

Key words alcohol aggression fish prior residence territoriality

An account of this work was presented by Dr Figler at the Second Biennial Meeting of the International Society for Research on Aggression in Paris 1976

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## INTRODUCTION

One common feature of the behavior of territorial species of animals is what has been termed the prior residence effect [Braddock 1949 Denny and Ratner 1970] The term refers to the dominance advantage of a territorial resident over an intruder Recently this effect has been demonstrated in the jewel fish Hemichromis bimaculatus [de Boer and Heuts 1973 Figler Klein and Peeke 1976] It was shown that a territorial encounter between a resident and an intruder eventuates in significantly more dominance decisions in favor of the resident In other experiments with H bimaculatus Figler Dyer Streckfus and Nardini [1975] and Figler et al [1976] found that if two combatants from distinct aquaria meet in a third aquarium which has a cue similar to that in one of the two home aquaria the fish with this familiarity is significantly more dominant This finding has been termed the prior exposure effect by these authors

The mechanisms underlying these effects are unclear For instance is the residential dominance advantage due to the increased aggressiveness/decreased fear of the resident or decreased aggressiveness/increased fear of the intruder or some combination of these variables?

The present experiments were planned to shed light on this problem with the use of a pharmacological preparation and the highly territorial Convict Cichlid (Cichlasoma nigrofasciatum) also a member of the family Cichlidae This species was chosen because its agonistic behavior has been previously investigated in the field and the laboratory [Peeke et al 1975] alcohol uptake work has been completed [Peeke et al 1973 Peeke et al 1975] and alcohol dose agonistic response relationships have also been documented by Peeke and his coworkers in those studies

Doses consisting of 0 15% or 0 18% alcohol (per vol of aquarium water) produced higher levels of aggression (biting display frequency display time) toward an undrugged male conspecific intruder in a stimulus tube than either a no alcohol control group or residents immersed in a higher dose (0 30% or 0 33%) of alcohol Also the higher doses were associated with lower levels of aggression as compared to the no alcohol control situation [Peeke et al 1973 Peeke et al 1975] Therefore lower doses produced hyperaggression and higher doses elicited hypoaggression compared to controls in this paradigm designed to investigate territorial aggression

In the present investigation a prior residence situation like that of Figler et al [1976] was used to provide the territorial behavior in this species The doses of alcohol were administered independently to resident or intruder at levels that have been shown in past work to increase or decrease territorial aggression In this manner it was possible to alter the levels of aggression in the resident or intruder to ascertain changes in the prior residence effect For instance if the effect resides primarily with increased aggression in the resident a hypoaggression producing dose of alcohol administered to the resident should obliterate the effect

However if the effect is primarily a function of decreased aggression in the in truder administering a hyperaggression producing dose to the intruder also should alter the prior residence effect Since Peeke et al [1973] have previously shown that similar doses of alcohol change the level of aggression of territorial Convict Cichlids without markedly disrupting the organization of the agonistic sequence any alcohol produced changes cannot simply be ascribed to the elicitation of abnormal sequences of behavior Although a more direct method for determin ing the loci of the prior residence effect would be to carefully analyze the inter actions of undrugged combatants the available alcohol data lent themselves to a preliminary investigation of this problem

Two final notes First the initial experiment of this series was undertaken to demonstrate the prior residence effect in this species in a no alcohol situation as well as to provide baseline levels of aggression Second the present study is the first known one to investigate the effects of alcohol on the behavior of freely interacting fish

## MATERIALS AND METHODS

### Subjects

A total of 204 adult male Convict Cichlids C nigrofasciatum were used in the present studies They were either obtained from a commercial supplier or bred in our own laboratory They were held in a number of large community holding tanks before being transferred to individual aquaria (21 liters 41 X 21 X 26 cm) The fish were fed daily with live brine shrimp (Artemia salina) or dried fish food Water temperature was maintained at 23°C ± 2°C by a thermostatically controlled laboratory heating system

### Apparatus

The individual aquaria although of identical dimensions were of two different internal environmental configurations in order to enhance the distinctiveness of resident and intruder territories Both types of aquaria contained a coarse gravel substrate and a 7 6 cm diameter terra cotta pot placed on its side as a refuge at the far end of the tank The two environments differed in that one contained a fist-size terra cotta rock near the pot whereas the other contained a 9 cm high green plastic plant (resembling Fontinalis antipyretica) positioned in a similar manner

The various aquaria were so arranged that a fish could see only one neighbor whose tank was placed next to him with one short side touching This neighbor was always from another treatment (environment) condition but was never the neighbor which was met in the subsequent direct encounter This visual exposure to a neighbor has been successfully used in a similar study [Figler et al 1976] to reduce fright behaviors in the test situation behaviors which have been shown to

compete strongly with the elicitation of aggression in laboratory studies of fish [Barlow 1968] The other short side of the aquaria looked out into the laboratory with the two long sides being covered on the outside by brown cardboard Therefore the refuges of the two neighbors were as far apart as possible although one could see his neighbor from inside the pot

## Procedure

A series of seven experiments were conducted all identical in procedure except for the dose of alcohol used and whether the resident or intruder received it Fish were paired beforehand and matched for body size with pair members never differing by more than 5% in length The fish were allowed to establish territories for 5 days in these separate aquaria with pair members in distinct environmental conditions Again these future combatants never saw each other during the territorial establishment period

Six hours before the encounter the desired weight of alcohol (ethanol 95% USP) was added to the appropriate aquarium to give the required alcohol water concentration The procedure was the same as used in past research with similar doses [Peeke et al 1973 Peeke et al 1975] The blood level of ethanol in the fish was expected to reach 65% of the water concentration after a period of 6 hr Since doses of 0 0 15% 0 20% and 0 35% were used for either the resident or intruder (only one pair member could receive the drug) a possibility of seven different combinations were possible No drug used 0 15% drugged resident 0 15% drugged intruder 0 20% drugged resident 0 20% drugged intruder 0.35% drugged resident and 0 35% drugged intruder A slightly higher dose (0 20%) than has been used in previous studies to increase aggression was also included in the present study This third dosage level was included in order to determine *the upper dose limits for the hyperaggression effect*

On the day of testing 6 hr after the alcohol if any had been added to one of the aquaria both pair members were netted and removed from their resident tanks During this few second handling period an opaque white Plexiglas partition was inserted into the resident fish s aquarium dividing it into two equal compartments The pair members were then placed into the *resident s* tank with the two fish being separated by the partition and the resident being in that half containing his refuge pot and other marker It seems reasonable to assume that the alcohol had little effect on the intruder in resident-drugged tests since Peeke et al [1973] have determined that alcohol uptake proceeds very slowly across a 6–8 hr period In the present studies the undrugged intruder was in an alcohol solution for a duration well under a total of 30 min (adaptation and testing) a duration of exposure presumably allowing little time for marked uptake to occur The experiments were arranged so that there were a similar number of residents from the rock condition as from the plant condition to control for any differential effects *of these* stimuli as territorial cues

After 15 min the partition was lifted and the fish met in a direct encounter As described more thoroughly in past studies [de Boer and Heuts 1973 Figler et al 1975 Figler et al 1976] a pair member was considered to be showing dominance behavior if it bit or butted the other fish and this behavior was associated with or was immediately followed by an escape movement by the attackee Also considered as dominance behaviors were a frontal or lateral display or tailbeat followed by a sudden and/or accelerated escape movement (fleeing or submissive behavior) A pair member was determined to have established a dom inance relationship (ie declared the victor) if it showed six consecutive dominance behaviors as in de Boer and Heuts [1973] Figler et al [1975] and Figler et al [1976] If an encounter did not produce any agonistic behavior in pair members within 30 min the testing was terminated Also recorded along with the final dominance decision was the time which elapsed from the lifting of the partition to the attainment of dominance criterion and the pair member which bit first in the encounter

## RESULTS

The results as presented in Table I show that alcohol does not appreciably change the prior residence effect when the intruder is drugged but does produce changes when the resident receives either the 0 20% or 0 35% dose In the no alcohol group 15 residents (94%) dominated while only 1 was defeated a highly significant prior residence effect ($p < 0\ 01$) * When the resident received 0 15%

**TABLE I Summary of Data From Alcohol Prior Residence Experiments in Convict Cichlids (Cichlasoma nigrofasciatum)**

| % Alcohol | | Total pairs | Bit first | | Victor | | Mean bout duration (sec) |
|---|---|---|---|---|---|---|---|
| | | | Resident | Intruder | Resident | Intruder | |
| 0 00 | Both | 16 | 13 | 1 | 15 | 1 | 416 25 |
| 0 15 | Intruder | 8 | 5 | 1 | 8 | 0 | 174 63 |
| 0 15 | Resident | 11 | 10 | 0 | 11 | 0 | 199 36 |
| 0 20 | Intruder | 15 | 11 | 2 | 15 | 0 | 274 53 |
| 0 20 | Resident | 22 | 19 | 2 | 14 | 8 | 344 16 |
| 0 35 | Intruder | 8 | 3 | 5 | 8 | 0 | 139 75 |
| 0 35 | Resident | 22 | 17 | 1 | 14 | 8 | 314 86 |
| | TOTAL | 102 | 78 | 12 | 85 | 17 | |

The reported probability values are two-tail d and are based upon the Fisher Exact Probability test [Siegel, 1956] unless otherwise specified

alcohol all 11 of them dominated the intruders ($p < 0\ 01$) However when the resident was immersed in either a 0 20% or 0 35% alcohol solution they dominated in only 64% of the encounters (14 out of 22 $\chi^2$ (1) = 2 27 $p > 0.05$) In other words there was no significant prior residence effect when residents received either of the higher doses

Considering the drugged intruder data it is noteworthy that no one intruder in any of the three alcohol groups achieved dominance That is the undrugged resident consistently achieved 100% dominance in the 0 15% ($p < 0\ 01$) 0.20% ($p < 0\ 01$) and 0 35% ($p < 0\ 01$) groups respectively

Also summarized in Table I is the finding that the resident (drugged or undrugged) bit first significantly more than intruders in an encounter ($p < 0\ 01$) when the data were pooled across groups This relation held for all groups except the 0 35% drugged intruder group where only three out of eight residents bit first ($p > 0\ 05$) It should be noted here that in Table I there is in many cases a discrepancy between the numbers in the Bit First and Victor columns Such a discrepancy is due to situations where the combatants bit virtually simultaneously or when the initial bite took place when the observer s line of vision was interrupted by a pot plant etc In such cases therefore no decision on which fish bit first could be made

Another significant finding is that biting first in an encounter reliably eventuated in dominance except in the 0 35% drugged intruder group ($p > 0\ 05$) Bitin first predicted dominance in the no alcohol ($p < 0\ 01$) 0 15% drugged resident ($p < 0\ 01$) 0 15% drugged intruder ($p < 0\ 05$ one tailed) 0 20% drugged resident ($\chi^2(1) = 9\ 52$ $p < 0\ 01$) 0 20% drugged intruder ($p < 0\ 01$) and 0 35% drugged resident ($\chi^2(1) = 9\ 00$ $p < 0\ 01$) groups respectively

The longest mean bout duration occurred in the no alcohol group ($\bar{X} = 416.25$ sec) with the 0 20% drugged resident ($\bar{X} = 344\ 16$ sec) 0 35% drugged resid nt ($\bar{X} = 314\ 86$ sec) and 0 15% drugged resident ($\bar{X} = 199\ 36$ sec) groups following in that order A Kruskal Wallis one way analysis of variance showed no signifi a t bout duration differences between these groups ($\underline{H} = 6\ 19$ $p > 0\ 05$)

The no alcohol and drugged intruder groups (0 15% 0 20% 0 35%) bout durations were then compared using the Kruskal Wallis test with a highly significant treatment effect being revealed ($H = 13\ 24$ $\underline{p} < 0\ 01$) Subsequent Mann Whitney $U$ tests showed that the no alcohol group had a significantly longer bout duration than the 0 15% drugged intruder ($U = 21$ $p < 0\ 02$) 0 20% drugged intruder ($U = 63\ 5$ $p < 0\ 05$) and 0 35% drugged intruder ($U = 14$ $p < 0\ 002$) groups respectively There were however no significant differences in bout duration between any two of the drugged intruder groups ($p > 0\ 05$)

## DISCUSSION

These results demonstrate profound effects of alcohol on the territorial dominance behavior of C nigrofasciatum in a free interaction situation If an intruder

s given alcohol he will not displace the resident even if the dose is one that has been shown in another situation to create higher levels of a number of the components of the aggressive behavior of this species The intruder is affected detrimentally as shown by the shorter bout durations possibly indicative of a less intensive attempt to displace the resident The resident is affected by a higher but not a lower dose of alcohol It is interesting to note that the effects of the 0 20% resident dose were almost indistinguishable when compared to the 0 35% resident dose Therefore the 0 20% dose is apparently large enough to produce hypo-a gression like doses of 0.33% or 0 35% [Peeke et al 1973 Peeke et al 1975] The higher doses which gave no indication in this experiment or previous ones [Peeke et al 1973 Peeke et al 1976] of being behaviorally debilitating in any general way abolished the dominance advantage provided by prior residence in the environment

Also of interest are the parallels between the present data and those derived from prior residence and prior exposure studies with the jewel fish [de Boer and Heuts 1973 Figler et al 1975 Figler et al 1976] another species of the family Cichlidae In all of the above studies a residence effect was demonstrated with this phenomenon being experimentally created and with other factors having been controlled (eg size past experience) In general the resident bites first in an encounter with this variable being a reliable predictor of dominance The qualitative similarities in the agonistic sequence of the two species also include gillcover erection lateral display biting butting and jawlocking These behaviors common to the family have been previously noted by Baerends and Baerends van Roon [1950] As in the jewel fish studies the present encounters began slowly with very staccato locomotor behavior (fear) prevailing during the first few moments Biting was then interspersed with head to tail lateral displays gill cover erection and short duration jawlocks Although no quantitative measures were made of these agonistic behaviors it should be noted that head to tail lateral displays very common in the present studies were not seen in the earlier jewel fish studies (head to head laterals) and the long duration jawlocks characteristic of jewel fish encounters were not part of the Convict Cichlid agonistic repertoire Fighting typically ensued for a few minutes with one pair member suddenly breaking off and fleeing while being chased by the victor Until this sudden termination occurred it was not evident which of the combatants would be the ultimate victor [Figler et al 1976]

The present investigation provides support for the notion that the main determinants of the prior residence effect involve some change in the resident s behavior and/or morphological characteristics which accompany the establishment of a territory Of course the fact that the drugging of residents but not of intruders abolished the prior residence effect does not rule out a critical role of the intruder in producing these findings The intruder itself may be the key factor in producing this phenomenon by responding to some behavioral/morphological difference in the drugged resident Only further research can determine exactly

what behavioral/morphological changes are taking place during territorial establishment and subsequent encounters between resident and intruder These changes, however can occur without necessarily engaging in a dominance encounter with a conspecific prior to territorial establishment as shown in the above studies Of course it is not suggested that prior residence or exposure are the only variables important in the establishment and maintenance of dominance Factors such as the relative size of the opponents and past experience have been shown to be of primary importance [de Boer and Heuts 1973 Figler et al 1976]

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AGGRESSIVE BEHAVIOR
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# Attack by Female Mice on "Strangers"

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In this study the aggressive responses directed by small groups of female mice towards virgin pregnant and lactating female strangers, which were individually introduced into their cages were compared The results obtained show that except when lactating pregnant females are neither attacked much more often nor any more severely than virgin mice It is suggested that only the state of lactation favors the production of stimuli (olfactory) which release attack by female mice

Key words aggression, females, group lactation mice odors, pregnancy virgins

## INTRODUCTION

Maternal aggression in mice has been studied by a large number of workers [Beniest Noirot 1958 Gandelman 1972 St John and Corning 1973 etc) Some of these authors have discussed the utility of this behavior and conclude that aggressive behavior by the mother cannot be considered as having the function of protecting the young Our previous work demonstrated that lactating mice are very vigorously attacked when they are introduced as intruders into cages occupied by a large number of other females [Haug 1972b] Support for the contention that this type of aggression is influenced by a pheromone present in the mother s urine has been obtained [Haug 1973b]

Pregnant females in particular when living with a male [Noirot et al 1975] or when kept in isolation [Goyens in press] appear equally aggressive toward

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foreign males and females, when presented together or individually We thought that it would be of particular interest to verify if pregnant mice are also capable like lactating mothers of stimulating attacks by groups of females For this reason the incidence of aggressive encounters produced in small groups of females in response to the introduction of virgin pregnant or lactating strangers was studied

## MATERIALS AND METHODS

### Housing Conditions of Mice Having the Strangers Introduced Into Their Cages

Female mice of the Swiss strain (270) aged around 30 days were divided into groups of three animals The mice were housed in Makrolon cages measuring 33 X 12 X 18 cm Bedding was renewed every week the final change being done 24 hours before the start of behavioral testing All females received food and water ad libitum

### Housing Conditions of Female Strangers

Pregnant females (PG) Thirty adult females were housed in small groups *of two animals in one of the compartments of a divided cage measuring* 33 X 12 X 18 cm the other side being occupied by a male A perforated partition separated the two halves of the cage permiting an exchange of sensory stimuli between the mice Thirty six hours later the central partitions were removed allowing contact between the males and the females They remained in this condition for 24 hours in order for the males to impregnate their partners After this time the females were segregated to their original groups of two until the time of behavioral testing

Lactating females (LAC) The procedure used above in which females are exposed and rendered pregnant in batches of 30 can also be used to produce lactating females Females remained in groups of two just prior to parturition At the time of parturition each female was isolated in an individual cage

At the end of this period each litter was adjusted to eight pups consisting of four males and four females

Virgin females (VG) Thirty females were housed for a 24 hour period in the presence of a male castrate then kept as pairs in a cage except at the time of behavioral testing

### Experimental Procedure

Three series of 30 experimental aggression tests were carried out for each of 30 groups of three females using 30 female strangers consisting of ten virgin mice ten pregnant mice and ten lactating mice A period of one week separated the start of each new series of tests The grouped animals were approximately 3 months old at testing

First series ($W_1$) The grouped females were randomly tested for aggression ainst strange conspecifics introduced into their cage Two procedures of random ation have been used The first consisted of dividing the 30 experimental groups f females arbitrarily into six subgroups in order to perform six aggression trials ach day over five consecutive days in the second case we allocated each selected ubgroup to one of the three experimental treatments which were exposure to ) virgin females (VG1) b) pregnant females (PG1) and c) lactating females LAC1) All these trials are carried out daily between 1 and 7 PM The duration of each test could vary from 30 minutes to one hour as has been described previously [Haug 1972a b 1973a b] When a strange female (virgin pregnant or lactating) was severely bitten during the 30 minutes after being first introduced into the cage the latency was measured The number of bites given by the females to the strangers was then recorded during the subsequent period of 30 minutes On the other hand if at the end of a 30 minute period the newcomer female had not been submitted to any agressive responses she was either returned to her litter or her initial cage partner In this case the only measure obtained was the total time (in seconds) spent with the other females

Second series ($W_2$) In this experimental series the aggressive responses of 30 new groups of mice with respect to the stranger females introduced in their cages were recorded Besides virgin females (VG2) the grouped females were sub mitted to the presence of pregnant mice (PG2) or mice in the second week of lactation (LAC2)

Third series ($W_3$) In this last series of behavioral tests the aggressive responses elicited by the introduction of virgin mice (VG3) of mice in the third week of lactation (LAC3) or mice at the end of pregnancy (PG3) were recorded

## RESULTS

### Comparison of the Total Number of Attacks Directed by Group Housed Females Towards Virgin Pregnant or Lactating Mice (Tables I–III Fig 1)

Comparisons of categories employed Student s modified test The groups of animals tested in the first ($W_1$) and the third ($W_3$) experimental series did not differ significantly with respect to their numbers of attacks In contrast animals tested during the second series ($W_2$) were very much more aggressive towards lactating mice (LAC2) than towards pregnant mice (PG2) or virgin females (VG2) This was significantly the case in both comparisons VG2 – LAC2 ($P < 0.001$) and LAC2 – PG2 ($P < 0.001$) It is interesting to note however that numbers of attacks did not differ in groups receiving successively at one week intervals virgin or pregnant intruders The only significant difference was with respect to groups in the presence of lactating mice (LAC1 – LAC2 $P < 0.01$ LAC? – LAC3 $P < 0.01$) which confirms previous results [Haug 1972b]

**TABLE I Numbers and Latencies of Attacks**

| Series | Treatment | Number of tests | Mean number of attacks ± standard errors | Mean latency of at[illegible] ± standard erro[illegible] |
|---|---|---|---|---|
| $W_1$ | VG1 | 10 | 7 7 ± 2 70 | 1 172 ± 214[illegible] |
| | LAC1 | 10 | 16 3 ± 4 20 | 585 ± 199[illegible] |
| | PG1 | 9[a] | 16 3 ± 3 11 | 745 + 217[illegible] |
| $W_2$ | VG2 | 10 | 9 1 ± 2 83 | 1 018 ± 09[illegible] |
| | LAC2 | 10 | 31 4 ± 2 95 | 98 ± 37[illegible] |
| | PG2 | 10 | 12 0 ± 4 09 | 875 ± 237[illegible] |
| $W_3$ | VG3 | 10 | 8 4 ± 2 21 | 1 038 ± 217[illegible] |
| | LAC3 | 10 | 15 4 ± 3 24 | 624 ± 215[illegible] |
| | G3 | 9[b] | 12 2 ± 3 31 | 711 ± 246[illegible] |

[a]One mouse not pregnant The statistical comparison is therefore based on the results obtained by nine experimental groups

[b]For one mouse parturition happened on the 19th day of pregnancy whereas fo[illegible] all the other females this happened regularly on the 21st day This mouse was [illegible] eliminated from the experimental analysis

**TABLE II Numbers of Attacks A) Comparisons Between the Different Treatments**

| $W_1$ | $W_2$ | $W_3$ |
|---|---|---|
| VG1 LAC1 t = 1 75 | VG2 LAC2 t = 4 51* | VG3 LAC3 t [illegible] |
| VG1 PG1 t = 1 72 | VG2 PG2 t = 0 58 | VG3 PG3 t [illegible] |
| LAC1 PG1 t = 0 00 | LAC2 PG2 t = 3 94* | LAC3 PG3 t - [illegible] |
| dl = 26 | dl = 27 | dl = 26 |

*P < 0 001

**TABLE III Numbers of Attacks B) Comparisons in the Same Treatment**

| Lactating mice | Pregnant mice | Virgin mice |
|---|---|---|
| LAC1 LAC2 = 2 91* | PG1 PG2 t = 0 83 | VG1 VG2 t = 0[illegible] |
| LAC1 LAC3 = 0 17 | PG1 PG3 t = 0 77 | VG1 VG3 t = 0[illegible] |
| LAC2 LAC3 = 3 08* | PG2 PG3 t = 0 03 | VG2 VG3 t = 0[illegible] |
| dl = 27 | dl = 25 | dl = 27 |

* P < 0 01

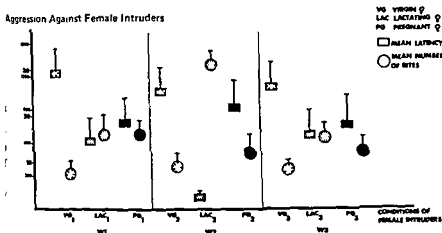



Fig 1 Aggression directed by groups of female mice against virgin (VG) pregnant (PG) and lactating (LAC) strangers

**Comparison of Latencies of Attack Directed by Grouped Females Towards Virgin Pregnant or Lactating Mice (Tables I IV Fig 1)**

For the purpose of statistical comparison the latencies were totals expressed in seconds The mean values given are times after introduction and are given in and the corresponding Figure 1

During the first experimental series ($W_1$) there was a significant decline in latency in groups subject to lactating mother intruders with respect to those subjected to virgin females (VG1 – LAC1 $P < 0\,02$) This single difference was not evident in the third series of tests In contrast in the groups in the second series ($W_2$) attacks were directed more quickly towards intruding lactating females than towards virgin females (VG2 – LAC2 $P < 0\,01$) or pregnant females (PG2 – LAC2 $P < 0\,01$)

It was also noticed that between group variation latencies were slight with respect to grouped animals submitted only in the presence of virgin females or with pregnant females whereas there was a significant difference between the means over the groups in the presence of lactating females (LAC1 – LAC2 $P < 0\,02$ LAC2 – LAC 3 $P < 0\,02$)

## CONCLUSION AND DISCUSSION

In previous work [Haug 1973a b] evidence was obtained of a stimulatory action of particular odors on fighting behavior in mice which act in such a way as to alter behavior in grouped females at the time of introduction of female

**TABLE IV Latencies of Attack A) Comparisons Between the Different Treatments**

| $W_1$ | | | $W_2$ | | | $W_3$ | | |
|---|---|---|---|---|---|---|---|---|
| VG1 | LAC1 | t = 2 14* | VG2 | LAC2 | t = 3 39** | VG3 | LAC3 | t 1[illegible] |
| VG1 | PG1 | t = 1 38 | VG2 | PG2 | t = 0 52 | VG3 | PG3 | t 0[illegible] |
| LAC1 | PG1 | t = 0 51 | LAC2 | PG2 | t = 2 87** | LAC3 | PG3 | t 0[illegible] |
| | dl = 26 | | | dl = 27 | | | dl = 26 | |

* P < 0 02
**P < 0 01

**TABLE V Latencies of Attack B) Comparisons in the Same Treatment**

| Lactating mice | | | Pregnant mice | | | Virgin mice | | |
|---|---|---|---|---|---|---|---|---|
| LAC1 | LAC2 | t = 2 13* | PG1 | PG2 | t = 0 39 | VG1 | VG2 | t 0[illegible] |
| LAC1 | LAC3 | t = 0 15 | PG1 | PG3 | t = 0 09 | VG1 | VG3 | t 0[illegible] |
| LAC2 | LAC3 | t = 2 09* | PG2 | PG3 | t = 0 49 | VG2 | VG3 | t 0[illegible] |
| | dl = 27 | | | dl = 25 | | | dl = 27 | |

*P < 0 02

intruders These aggressive responses are more intense when the strange female is lactating There is some evidence favouring the suggestion that a chemical influence is apparent in this phenomenon It is possible to make mice more aggressive in the presence of a strange female by housing it with a lactating mother [Haug 1973a] One obtains a similar effect by introducing an ovariectomized female stranger which has previously been marked with urine from a lactating mouse into groups of females [Haug 1973b] All aggressive behavior can usually be suppressed in grouped mice by olfactory bulbectomy [Haug 1972]

In this study the possibility that the aggressive behavior that grouped females display towards lactating intruders would also be facilitated when they are put in presence of strange pregnant females was investigated It has been suggested by many authors [Le Magnen 1952b Averseng Buhot in preparation] that it seems possible to differentiate a pregnant female mouse from a virgin female by odor The results obtained here do not favor this hypothesis At all time intervals tested the pregnant females introduced into groups of resident mice were not significantly more attacked than were virgin mice On the other hand attacks made by grouped females towards lactating mice were more violent than those directed towards virgin or pregnant mice Lactating mice in the first week of this process ($W_1$) were attacked with a much shorter latency period than virgin females However the major differences encountered were between mice in the second

week ($W_2$) of lactation and the other experimental categories with respect to both number of attacks and latencies

The results reported here confirm that the aggressive responses of grouped mice to intruders are only intense if the intruders are strange lactating females As the presence of a urinary maternal releasing factor has been postulated [Haug 1973b] it is suggested that such a factor is not produced during the pregnancy period despite a greater secretion of sex steroids [Choudhary and Greenwald 1969 Finn and Martin 1969 McCormack and Greenwald 1974]

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AGGRESSIVE BEHAVIOR
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# Mediating Factors in Chick Social Pecking I Effects of Isolation, Imprinting, and Peer Contact

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Two experiments examined the influence of periods of social isolation on rates of intersubject pecking in pairs of domestic chicks. Of central interest was the effect of an imprinting condition wherein single birds were reared with either a red or green styrofoam object In the first experiment imprinted subjects were given social pecking tests in the absence of the imprinting object, while in the second study the tests for social pecking were conducted in the presence of one of the imprinting objects. In the latter test the object was familiar to one bird of a pair but was novel to the other animal. The results of both experiments showed that the rate of intersubject pecking of the imprinted subjects was intermediate to and statistically different from both the low pecking rate of chicks reared in pairs and the high pecking rate of chicks reared in total isolation The presence of a familiar object during tests in the second study seemed to serve as a secure base since chicks that had been reared with that object exhibited more social pecking than did chicks that were unfamiliar with the object. However regardless of the provision of the object the social pecking of the imprinted chicks again fell on a point intermediate to the other groups. Hypotheses concerning a) intolerance of figure-ground movement and b) sheer stress of isolation were ad vanced to account for these results.

Key words: chicks, imprinting isolation pecking peers, secure base

## INTRODUCTION

Short periods of social isolation result in heightened conspecific pecking in certain precocial hatchlings This intersubject pecking has been attributed to an aggressive motivation based on the force of the peck in ducklings [Hoffman et al

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1974] the reaction of the recipient of the peck in ducklings [Hoffman and Boskoff 1972 Hoffman et al 1975] and peck locus in chicks [Rajecki et al 1976 1977a] In an effort to identify factors that mediate the exaggerated pecking of former isolates Hoffman et al [1975] reared some ducklings with animated foam rubber objects This imprinting procedure produced social pecking rates that were much lower than those emitted by total isolates but which were statistically indistinguishable from rates emitted by ducklings reared in pairs Based on this finding Hoffman et al [1975] concluded that the experience of being reared with a mechanical imprinting object had the same consequence as being housed with a conspecific and suggested that both conditions lead to the same general state of nonaggressiveness in the duckling

For all the merit of the Hoffman et al [1975] approach the operational definition of aggressive responses in their research bears examination That procedure focused the observer on the target of the peck rather than on the pecking animal pecks were scored as aggressive only when they caused the withdrawal of the recipient Now while the behavior of the recipient of pecks is certainly interesting exclusive concentration on the victim s reactions may have limitations as an indicator of the disposition of the aggressor because even the strongest of aggressive motivations may not lead to victimization a point made clear by the finding of Hale [1948] that whereas less than 1% of social pecks were ignored by recipients in groups of normal hens fully 58% of such pecks were ignored in groups of debeaked hens It seems the debeaked hens in Hale s study were no less motivated than normals to dominate one another but merely were less effective in doing so due to the debeaking

The current tests with domestic chicks were a further investigation of experiential factors that mediate isolation induced social pecking in precocial birds While employing the general paradigm of the Hoffman et al [1975] study for the sake of comparison the methodology reported here had provisions to help clarify the issue raised above by concentrating on the peck response itself not on the reaction of the recipient of social pecking

Two experiments were conducted in which the social pecks of chicks reared with an imprinting object were compared to the respective responses of other subjects reared in total isolation or in pairs of conspecifics A basic distinction between these experiments was that in the first the imprinted chicks were tested for social pecking in the absence of the imprinting object *while in the second* the familiar object was present (for some birds) during pecking tests In all cases the frequency of locus of social pecking was recorded

## EXPERIMENT 1

### Method

Subjects The subjects were 36 White Leghorn chicks obtained from the Sunny side Hatchery (Oregon Wisconsin) on the day of hatching Since subjects were hatched communally and were transported to the laboratory in groups in cartons,

they had a small but unspecified amount of social experience prior to random assignment to rearing conditions Similarly all birds in the Hoffman et al [1975] research experienced conspecific contact prior to assignment to rearing conditions Earlier studies with chicks have shown that isolation produces comparable patterns and levels of social pecking in birds with or without prior visual and tactile exposure to conspecifics [cf Rajecki et al 1976 1977a] The sex of the birds was not determined each was marked on the head or the back with a felt pen for identification

An equal number of chicks was assigned to each of three experimental conditions In the first of these termed the social condition pairs of birds were reared communally in six cages For the second condition termed isolate 12 birds were reared individually in separate cages The final condition was termed the imprinted group in which 12 chicks were reared in separate cages Six of these cages were equipped with a suspended red block (see below) and the remaining six contained a suspended green triangle

*Housing units* Subjects were reared in 22 5 X 17.5 X 17 5-cm stainless steel cages that contained separate petri dishes filled with water and chick starter A 40 W bulb installed on the front mesh wall illuminated and heated each cage to 30 C The light cycle was set at 25 minutes on/5 minutes-off following an earlier procedure [Rajecki et al 1976]

For half of the imprinted subjects the cage was also equipped with a 7 X 7 X 3-cm styrofoam block painted red The block was suspended 3 cm from the center of the floor of the cage and was freely movable as a pendulum The remaining subjects in this condition were assigned to cages equipped with individual 7 X 7 X 3-cm styrofoam triangles painted green These objects were similar in configuration to those employed in earlier research on attachment in chicks [eg Wilson and Rajecki 1974 Zajonc et al 1974]

*Test schedule* Subjects were observed in a series of tests The first test (preference test) was primarily devoted to the question of whether chicks in the imprinting condition had generally formed an attachment to the imprinting target suspended in their particular cage For the sake of equivalent handling all birds in the other two conditions were also given a preference test as individuals The second test termed the social pecking test pitted two birds against one another The social pecking test constituted the measure of aggressive tendencies as influenced by the various treatments

*Preference test* Approximately 48 hours after assignment to rearing condition subjects were taken in random order from their cages and given a simultaneous choice test between a red block and a green triangle Approach responses were recorded in a 70 X 62 X 60-cm masonite test box that had a hardware cloth floor and one way observation windows installed along the full extent of the longer sides Illumination was provided by shaded 100 W bulbs anchored inside the unit A copy of each of the imprinting targets was suspended 3 cm from the floor at opposite ends of the box along the center line some 9 5 cm from the front and rear walls

For a preference test a subject was placed on the floor equidistant from both objects oriented in a way so that the midline of the body was perpendicular to a line drawn between the two objects During the five minute test distress calls were tallied by a voice key and the subject s locomotor responses were record d using a ten second time sample Every ten seconds the position of the bird was noted If the animal had reached an area 20 cm from one or the other of the targets it was assigned a score of 1 for that interval (for that object) If the chick was observed in an area 10 cm from the object it was assigned a score of 2 for that ten second interval (for that object) For time intervals when the animal had crossed neither threshold (or had returned to the starting area) a score of 0 was assigned Based on this scoring method preference scores could range from 0 to 60 for a given target

**Social pecking test** Approximately three hours after the administration of th preference test subjects were observed in the social pecking test that took pla e in an otherwise empty 22 5 X 17 5 X 17 5-cm galvanized iron cage The mesh front wall of the cage had been removed and was replaced with a pane of clear Plexiglas An amplitude sensitive voice key was installed near the test cag that automatically detected and counted vocalizations louder than 80 dB The general configuration of this test unit can be seen in Rajecki et al [1976 Fig 1] Illumination was provided by a floodlamp mounted some 1.5 m from the Plexi las front wall

For the social pecking test two subjects from the same rearing condition wer transported to the test unit in separate carrying cages It is important to note here that since subjects from the isolate and imprinting conditions inevitably en countered noncagemates in this test a control procedure was followed th t insured that the social subjects were not tested with their cagemates but rather with a stranger bird from some other pair of socially reared animals Subjects were placed in the unit simultaneously and were not given a period of adaptation before record keeping was begun

Each test was of ten minutes duration During that time the subjects peck responses were tallied using a hand held data panel the buttons of which were connected to an operations recorder This procedure recorded pecks by a partic lar bird that were aimed at the head body or foot region of its opponent or at any part of the test unit A single experienced observer was employed for all tests

## Results

**Preference test** The average weighted approach scores are presented in Table I For purposes of certain statistical contrasts four independent treatment groups were specified socials (n = 12) isolates (n = 12) imprinted birds reared wi h a red object (n = 6) and imprinted birds reared with a green object (n = 6) A 4 (X 2) analysis (representing rearing condition and object choice) of approach scores indicated that there was a significant effect for rearing condition overall

TABLE I Average Weighted Approach Scores and Distress Calls in the Preference Tests

| | Weighted approach score | |
|---|---|---|
| Rearing condition | Experiment 1 | Experiment 2 |
| Socials | 6 38 | 4 83 |
| Isolates | 10 34 | 13 23 |
| Imprinted chicks | | |
| Novel object | 0 75 | 6 22 |
| Familiar object | 33 75 | 26 78 |

F [3 32] = 5 52 P < 0 05) but no overall preference for one or the other object (F = 1.33 ns) However the imprinted birds showed a strong preference for the familiar object as reflected in an interaction between rearing condition and object choice (F [3 32] = 17 18 P < 0 01)

Social pecking test Average number of pecks per bird (per minute) at the various loci are shown in Table II Values for pecking were cast in a 3(X 4) analysis of variance representing rearing conditions and peck locus The average value over both birds of a pair served as the unit of analysis Of main interest is a comparison of the pattern of pecking by subjects assigned to the different treatment conditions It can be seen in Table II that isolate subjects made more pecks at the heads of their opponents than did birds from the social condition and that the imprinted subjects were intermediate to the other groups on this measure These marked differences produced an interaction between rearing condition and peck locus (F [6 45] = 7 97 P < 0 01) In fact post hoc analyses revealed that all conditions were significantly different from one another on head pecking at least at one tailed levels of significance (socials vs imprinted birds t [10] = 3 60 P < 0 01 imprinted birds vs isolates t [10] = 2 14 P < 0 05) Average numbers of distress calls (per minute per bird) emitted during tests of social pecking are also shown in Table II The result of a one way analysis of variance was a marginal effect for rearing condition on that measure (F [2 15] = 3 14 P < 0 10)

## Discussion

The major finding from the first experiment is that the rearing conditions produced differences in levels of social pecking Of special interest is the fact that the rate of head pecking by imprinted chicks was statistically distinguishable from the rates of both the social and isolate comparison conditions This finding suggests that the process of imprinting on an artificial object (for this species under these circumstances) does not produce the same level of nonaggressiveness as does cohabitation with a conspecific Still exposure to an imprinting object did lead

**TABLE II Average Responses (per minute) in Social Pecking Tests in Experiments 1 and 2**

Experiment 1

| | Rearing condition | | |
|---|---|---|---|
| Response category | Socials | Imprinted birds | Isolates |
| Head peck | 0 75 | 3 47 | 6 03 |
| Body peck | 0 25 | 0 34 | 0 74 |
| Foot peck | 0 25 | 1 50 | 1 39 |
| Cage peck | 2 40 | 1 29 | 0 71 |
| Distress call | 0 46 | 12 14 | 6 54 |

Experiment 2

| | Rearing condition | | | |
|---|---|---|---|---|
| | | Imprinted birds | | |
| Response category | Socials | Novel object | Familiar object | Isolates |
| Head peck | 2 35 | 4 32 | 6 27 | 8 89 |
| Body peck | 0 43 | 0 32 | 0 65 | 0 70 |
| Foot peck | 0 84 | 0 22 | 0 75 | 1 45 |
| Cage peck | 2 16 | 0 65 | 1 88 | 2 60 |
| Object peck | 1 24 | 0 65 | 1 68 | 2 39 |
| Distress call | 0 90 | 8 13 | 6 08 | 0 56 |

to fewer social pecks than did total isolation a finding generally in line with the results of Hoffman et al [1975]

The results of experiment 1 must be momentarily qualified however by the observation that the imprinted chicks gave the highest rate of distress calling during the social pecking test While it may be that this high rate was due to separation from the imprinting object it remains that the vocal behavior of these subjects may have precluded the emission of social pecks and that the rate of pecking for this group was due in part to an artifact As a check against this possibility a second experiment was conducted

## EXPERIMENT 2

The second study while generally a replication of the first provided an important extension During the social pecking tests of imprinted chicks green reared birds were pitted against red reared counterparts in the presence of a replica of either the green or the red imprinting object Testing of certain birds for social pecking in the company of the familiar object seemed a way to rule out the possibility that distress due to separation was responsible for peck rates for this

up in experiment 1 Further the provision of the imprinting object of one d of a pair permits an examination of the so called secure base phenomenon or research has demonstrated that an imprinted bird is more likely to show gression (ducklings [Collias and Collias 1956 Hoffman and Boskoff 1972]) ploration (chicks [Wilson and Rajecki 1974]) or approach to a fear provoking mulus (ducklings [Stettner and Tilds 1966]) in the presence of the imprinting ject than in its absence Therefore the influence of such a secure base on inter oject peck locus and rate in chicks was examined in the current work

ethod

Subjects The subjects were 108 White Leghorn chicks procured as in the st experiment To eliminate the chance that artificial identification marks on e head would elicit pecks to the head all of the current subjects were marked the back Birds were assigned to the following conditions socials (n = 28) lates (n = 24) imprinted subjects reared with a red object (n = 28) and im inted subjects reared with a green object (n = 28) The unequal sample size was e to subject availability Housing conditions were the same as in experiment 1

Test schedule and procedure As in the first study tests for social pecking llowed the open field preference test In this experiment the preference te t as not strictly necessary as a measure of the influence of prior exposure to an printin object since the effects of that exposure could be assessed in the social cking test itself Nevertheless this procedural step was retained to make the o experiments comparable Because of scheduling constraints the preference sts were conducted ranging from approximately 22 to 45 hours after the assign ent of subjects to rearing conditions For a given subject the social pecking test llowed within three hours of the earlier observation

The procedures for both tests were slightly modified For the preference tests new scoring scheme was introduced that involved three concentric 10 cm areas ound each target Therefore weighted approach scores could range from 0 to 0

For the social pecking test modifications included the installation of a red or een imprinting object on the rear wall (the one away from the observer) of the st cage As noted in this study pecking tests of imprinted birds always involved ixed pairs of animals from the red and green subconditions Half of these pairs ere tested with the red object present and half were tested with the green bject As a control for any general effect of the presence of objects all social nd isolate subjects were also tested with an object present (red in half the cases) n addition to the measures listed in experiment 1 the observer recorded pecks irected at the imprinting object itself Two observers were employed for each est and each manually recorded the distress calls of his assigned subject Manual oding was adopted because the voice key does not distinguish between individual ubjects The duration of the social pecking test in this experiment was reduced o five minutes

**Results**

**Preference test** The results of the preference test are presented in Table I The weighted approach score outcome is generally similar to that of the first experiment There was a main effect for rearing condition (F [3 104] = 10 23 P < 0 01) again indicating most responsiveness by the imprinted chicks and least by the socials And again there was an object choice by rearing condition interaction (F [3 104] = 15 76 P < 0 01) indicating that the imprinted animals were likely to approach the familiar object in preference to the novel one However the overall approach tendency of these particular subjects was lower than that in the first study which difference may be accounted for by the shorter exposure period prior to the test

**Social pecking test** Data from the social pecking tests are presented in Table II Overall there is a strong main effect for rearing condition on pecking in general (F [2 51] = 24 91 P < 0 01) and an interaction between rearing condition and peck locus (F [6 153] = 9 97 P < 0 01) indicating in part the expected heightened head pecking by the imprinted and isolate subjects Post hoc tests of pairs again revealed that on head pecking all groups were different (socials vs imprinted chicks t [40] = 3 46 P < 0 01 two tailed imprinted chicks vs isolates t [38] = 2 77 P < 0 01 two tailed)

When considered separately (and treated as individuals rather than pairs) the green and red reared imprinted animals did not differ on overall social pecking (F = 1 97 ns) In terms of the secure base question however there was a strong effect for the presence of the familiar or imprinted object as reflected in an interaction between test color and rearing condition (F [1 52] = 9 56 P < 0 01) This difference is illustrated in Table II in the lists of peck responses by animals tested with a novel or familiar object Clearly the secure base effect obtained in terms of group averages This pattern was also discernible when individual tests were considered In 19 of the 28 social pecking tests involving imprinted birds the winner of the test (gave more pecks than received) was the bird for which the object was familiar (z = 1 70 P < 0 05 one tailed)

The pattern of distress calling in this study is similar to that observed in experiment I It can be seen in Table II that the imprinted chicks emitted high rate of vocal responding even when tested in the presence of the familiar object (F [3 100] = 5 04 P < 0 01) On this measure the imprinted chicks tested with a familiar object did not differ from those tested with a novel object

## GENERAL DISCUSSION

A troublesome aspect of the current results is that they are not consistent with those of Rajecki et al [1976 1977a] regarding the relationship of distress calling to social pecking Rather than speculating further on this it is sufficient to say that additional data are necessary if a simple hypothesis is to be formulated

Nevertheless there is evidence from both experiments that the exposure of to imprinting objects resulted in the formation of attachments to those jects In subsequent tests it was determined that these imprinted birds were less ly to peck at one another than were totally isolated conspecifics but were more likely to exchange pecks than were their socially reared counterparts That s rearing experience with an imprinting object reduced this form of aggression n chicks, but did not lead to the same level of nonaggressivenes that was observed by Hoffman et al [1975] in ducklings in similar circumstances

The findings of the current researches along with the earlier work of Hoffman et al [1975] have led us to two different (although not mutually exclusive) hypo concerning the mediating influence of partial or total isolation on inter ject pecking in precocial birds The first of the hypotheses has to do with the experience of movement The isolated subject is denied visual contact with animate objects and sooner or later may become accustomed to the lack of environmental movement That is however much the animal was tolerant of or habituated to general environmental activity prior to isolation that habituation or tolerance may be lost as a consequence of the resting state of the receptors On the other hand chicks (or ducklings) reared with a cagemate or an imprinting object continue to experience the movement of something in the environment

It follows from this argument that the totally isolated chick upon encountering a mobile test mate might be reacting in large part to the very animatedness of it opponent In simple terms if even socially reared birds react to unfamiliar features of strangers and therefore peck at them more than they peck at familiar companions [cf Rajecki et al 1976 Zajonc et al 1975] truly isolated subjects may be reacting to the (by then) utterly unfamiliar feature of sheer movement The argument that one of the critical factors in social tolerance is a general tolerance of figure-ground movement is at least in line with findings that prior exposure to animated objects and other types of stimulation increases sociability (susceptibility to imprinting) in the test naive hatchling [cf Bateson and Seaburne May 1973 Graves and Siegel 1968 Polt and Hess 1966 Saegert and Rajecki 1973]

This first hypothesis may also account for the difference between the current findings and the Hoffman et al [1975] data In our study the styrofoam imprinting objects were movable but moved only when touched by the subject In the Hoffman et al [1975] method the imprinting objects were moved by a mechanical method which means that the object s motility was largely independent of the imprinted duckling It seems an interesting possibility that experience with unpredictable movement or movement uncorrelated with the subject s own behavior might be positively related to degree of tolerance of the spontaneous movements of conspecifics

The second hypothesis concerns the role of the general state of stress or distress that is produced by social isolation It is now known that the naive isolated

duckling is not merely reactive to its environment but seems to seek out conspicuous visual stimulation [see Bateson 1969 1973] Similarly recent work with chicks has shown that birds hatched and reared in complete visual and tactile isolation give a great many distress vocalizations and show other forms of disturbance [Rajecki et al 1977b] It is as if these animals found social isolation somehow unpleasant even though they never had any actual social experience

Therefore it may be the case that the general negative emotional state produced by isolation carries over to social pecking tests When chicks are placed with conspecifics they are quite likely to exchange pecks in any event and thus the isolate may peck at high rates because this tendency is magnified by the general state of arousal produced by isolation In this light it may be the case that the difference in level of aggression of the ducklings of Hoffman et al [1975] and our chicks is that the moving objects in the former study were more effective in precluding emotional reactions to isolation

In future research it should be possible in principle to separate these two hypothesized mediators of isolation induced aggression in hatchlings Further it might be useful to extend these analyses to isolation induced reactions in other species

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AGGRESSIVE BEHAVIOR
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# Catecholamines in Predatory Behavior: A Review and Critique

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A variety of strategies have been employed in assessing the role of catecholamines (CA) in predatory behavior the results of these various approaches are reviewed While it remains difficult to ascribe a single biologically significant role to CA at this time this may at least in part reflect measurement considerations problems in the widely varying experimental models, pharmacologic side effects, and failures to categorically distinguish the differing contributions of individual CA systems in the control of predation The potential role of such factors in determining the outcome of an experiment are reviewed and possible functional contributions of CA systems are suggested.

Key words attack, catecholamines dopamine norepinephrine predation

## INTRODUCTION

Predatory or quiet biting attack is a complex and highly distinctive series of events not only behaviorally but motivationally and psychobiologically (Moyer 1968) At a behavioral level it includes a silent stalking approach to the prey and a rapid consummatory response involving positioning of the forepaws and biting directed at the neck Motivationally it appears to be associated with feeding (Katz and Thomas 1977) although the motivation for stalking and killing may also in part be intrinsic to the predatory act (Myer and White 1965 Van Hemel 1972) At the level of central nervous system (CNS) neuropsychophar

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macologic evidence exists for cholinergic facilitation of this behavior (Bandler 1969 1970a b Igic et al , 1970 Berntson and Leibowitz 1973 Gay et al 197 Hoffmeister et al 1964 Katz and Thomas 1974 Katz 1976a b McCarthy 1966 Miczek 1976 Smith et al 1970 Vogel and Leaf 1970 Wnek and Leaf 1973) and quite possibly for serotonergic involvement in its inhibition (Sheard 1969 Ferguson et al 1970 DiChiara et al 1971 note however Valzelli and Bernasconi 1972 Dubinsky et al 1973 Vergnes et al 1973 Sakata et al 1975 Miczek et al 1975 McCarty et al 1976)

While much evidence suggests that catecholamines (CA) i e norepinephrine (NE) dopamine (DA) and possibly also epinephrine (E) (major pathways for these transmitters are shown schematically in Fig 1) also influence the occurrence of predatory attack the precise involvement of these systems has yet to be fully elucidated In fact many drugs with presumably similar effects upon the CNS disposition of catecholamines produce varying and often diametrically opposed effects upon a given model or models of attack and few experiments exist whose findings have not been contradicted or qualified by other closely related experiments The present review was prompted in part by current dif

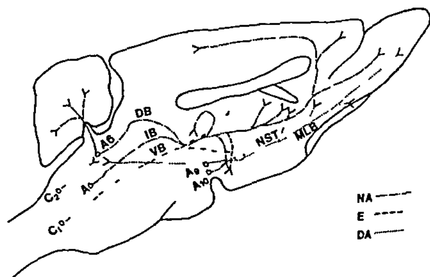



Fig 1 Major known and postulated CA pathways in the rat brain NA) Noradrenaline E) epinephrine DA) dopamine $C_1$ and $C_2$ are E-cell bodies as identified by Hokfelt et al. (1974) with pathways as postulated by the author $A_6$) Locus coeruleus (Ungerstedt 1971) $A_9$) substantia nigra $A_{10}$) interpenduncular nucleus Postulated $A_9$ to $A_6$ pathway from descriptions in Sakai et al (1977) DB) dorsal NA bundle IB) intermediate NA bundle (Jacobowitz 1973) VB) ventral bundle (probably contains both NA [Ungerstedt 1971] and E [Hokfelt et al 1974]) NST) nigrostriatal path from $A_9$ MLB) mesolimbic path from $A_{10}$ Spinal NA and E paths not included in diagram Figure 1 adapted from Ungerstedt (1971) and Lindvall and Bjorklund (1974)

ferences in experimental outcomes and in part by a variety of recently published experiments from a number of laboratories including our own which had not been summarized or examined in the context of previously published neuro and psychopharmacologic findings

A number of recent reviews have touched upon various aspects of predation (Avis 1974 Johansson 1974 O Boyle 1974 Reis 1974 Polsky 1974 Rossi 197 Barr et al 1976) The present paper is intended as an expanded and updated supplement to these reports It might be noted however that previous reviews have generally concluded that one or more CA serves an inhibitory role in predation Central adrenergic mechanisms appear to inhibit predatory ag gression (Reis 1974) One might conclude that some adrenergic mechanism suppresses the predatory response (Avis 1974) The present review was also prompted in part as a response to this conclusion While this view may be valid this validity may in part rest upon oversimplifications of some of the complex issues which are inherent in the measurement of aggression and its chemical cor relates These problems deserve comment and discussion

Finally in the interest of resolving several apparent disagreements regarding the roles of central catecholamine systems in predation we wished a) to provide an overview of past and current approaches to the problem b) to summarize the results of these approaches and c) to offer critical assessment of some of the fa tors which might have contributed to current differences e g species dif ferences measurement considerations pharmacologic effects or problems in the definition of attack

A relatively small number of strategies may be employed in the investigation of the neurochemical coding of a given behavior At any given time these strate gies are primarily a function of our understanding of how nerve cells communi cate information to other effector organs i e of our understanding of the synaptic transmission process At present these strategies include the applica t on either systemically or centrally of agents known to facilitate pre and post synaptic activity and the application of agents known to interfere with the trans mission process In both cases altered patterns of attack remain the major depen dent variable Finally it is possible to correlate naturally occurring differences (either steady state or turnover) in CNS neurotransmitter levels with differing patterns of behavior Each of these approaches has been employed with varying degrees of success in the investigation of predatory attack and while each ap proach carries with it certain inherent pitfalls – e g drugs that diminish preda tion may do so through motor impairment and turnover differences are essen tially presynaptic in nature while postsynaptic activation is a requisite for neural firing – the results of all approaches taken together offer a tentative but scienti fically reasonable and prudent description of the central control of predatory and other behaviors The results of each approach will be presented in course as will its attendant hazards In addition the present review will offer a tentative summary of the possible roles for central CA paths in predation

## RESULTS OF FACILITATING CA NEUROTRANSMISSION

The first section of this paper will review the effects of agents believed to potentiate postsynaptic receptor activation Agents known to produce this effect include psychostimulant drugs such as amphetamines iminodibenzyl antidepressant monoamine oxidase inhibitors and exogenous neurotransmitters

### Amphetamines

Amphetamines and related psychostimulants (e g methamphetamine methylphenidate) are known to have several CA potentiating activities In addition to potentiating the release of CA from presynaptic stores (Stein 1968 Stein and Wise 1969) they also inhibit synaptosomal reuptake (Glowinski et al 1966 Fuxe and Ungerstedt 1968 Taylor and Snyder 1970) and inhibit oxidative deamination by mitochondrial monoamine oxidase (Stein 1964 Glowinski et al 1966 Rutledge 1970) Any of these actions might separately serve to increase the occupation of postsynaptic receptors and their interaction results in strongly potentiated CA neurotransmission

Initial reports suggested that the predatory behaviors of the rat were inhibited by amphetamines (Karli 1958 1959 1960) and this result has been confirmed and expanded by numerous subsequent investigators using both amphetamines and related psychostimulant drugs (e g methylphenidate pipradol methamphetamine) (Horovitz et al 1965 1966 Horovitz and Leaf 1966 Horovitz 1966 Barnes, et al 1967 Kulkarni 1968 Karli et al 1969 Leaf et al 1969 Sofia 1969b Panksepp 1971 Valzelli and Bernasconi 1971 Ueki et al 1972 Kamei et al 1975 Valzelli and Bernasconi 1976 Gay et al 1976) In general the dosages of drug employed were considerably below those known to induce ataxia or motor stereotypy although it should be noted that Janssen et al (1962) claimed to find attack inhibition by amphetamine only when accompanied by motor impairment

At least for the specific model of spontaneous muricide the results generally suggest inhibition of attack with d amphetamine approximately eight times as active as its l isomeric forms The synaptosomal reuptake studies of Taylor and Snyder (1971) in which d amphetamine produced a differential blockade of CA reuptake into cortically derived synaptosomes while d and l amphetamine were equipotent in inhibiting reuptake from striatal synaptosomes and subsequent behavioral studies that confirmed these potency ratios suggest an adrenergic inhibitory mechanism (Malick 1975) This isomeric behavioral relationship may however be misleading (Bunney et al 1975 Holmes and Rutledge 1976) Studies involving NA and DA release or the suppression of firing in local CNS populations of aminergic neurons suggest diametrically reversed relationships e g d and l amphetamine are equipotent in suppressing the firing of neurons at the locus coeruleus but d amphetamine is considerably more potent than l

amphetamine at the substantia nigra (Bunney et al 1975) Therefore other CA such as DA or possibly E are not necessarily excluded Furthermore recent neurochemical studies indicate a possible involvement of still other amine systems for example serotonin (Fuxe and Ungerstedt 1970 Geyer et al 1975 Scheel Kruger and Hasselager 1974) or acetylcholine (Deffenu et al 1970 Hemsworth and Neal 1968) The inhibition of muricide is also to a large degree model-dependent Amphetamines are significantly less effective in inhibiting the muricide response in bulbectomized rats (Malick 1976) although this response is suppressed at high dosages Moreover amphetamines have been reported to facilitate a variety of other predatory behaviors For example in addition to suppressing the killing response of one behaviorally specific type of rat (i e the muricidal rat) amphetamines also induced a killing response in a second behaviorally distinctive rat (the normally indifferent rat) (Valzelli and Bernasconi 1976) Amphetamines also facilitated normally occurring murine prey killing (McCarty and Whitesides 1976) and potentiated brain stimulated predation in cats (Sheard 1967 MacDonnell and Fessock 1972) Since both experiments on feline prey killing involved cats that did not normally kill there is a conceptual similarity to the induction of killing seen in the indifferent rats in this last report The report of MacDonnell and Fessock is of particular interest since it offered independent assessment of drug effects upon attack initiation and attack velocity While amphetamines suppressed the initiation of attack (latency from stimulation onset to the initial approach component) they also facilitated on going attack sequences (nonetheless the generality of this finding may be limited (Sheard 1967)) It may be seen that amphetamines may possess behaviorally complex effects producing both inhibition and excitation depending upon many factors including species drug dosage and the measurement of "trigger or approach aspects of attack It is clear that the actions of amphetamines are at least in part dependent upon both the models and measures of attack employed

Two points should be noted regarding the present results and their relation to the neuropharmacology of amphetamine like drugs We have noted that amphetamines may affect neurotransmission in other CNS aminergic systems for example they are also known to release serotonin a neurotransmitter that may directly inhibit predation (Fuxe and Ungerstedt 1970 Scheel Kruger and Hasselager 1974 Geyer et al 1975 Reis 1974 Holmes and Rutledge 1976) Further amphetamines may produce their effects indirectly through an appetite mechanism amphetamines produce an anorexic response and this may therefore reduce predation through a reduction of appetite It has been shown (Polsky 1974 Rossi 1975 Katz and Thomas 1977) that appetitive factors may modify predatory attack behavior and amphetamines may therefore affect predation in this way Moreover amphetamines may also produce a food aversion (Berger 1972) thus lowering the likelihood of attack This is especially true in

situations where within subjects designs or repeated testing is used (Gay et al 1975) Barr and his associates (1976) also noted the possibility of an appetitively mediated pharmacologic suppression of killing

It may be possible to control for both neurochemical side effects and appetitive factors via appropriate behavioral and biochemical manipulations For example it would be possible to control for serotonergic involvement in amphetamine effects by comparing the effects of amphetamine in normal rats and rats pretreated with 5 7 dihydroxytryptamine a neurotoxin with a highly selective action upon serotonin containing neurons It might also be possible to treat rats with 5HT active amphetamine analogues such as fenfluoramine which are anorexia producing but which have few established effects upon central CA systems Finally a limited use of repeated testing and the inclusion of explicit aversion control groups may minimize other extrinsic factors such as food aversion

## Antidepressants

Clinically effective antidepressants (tricyclic antidepressants and monoamine oxidase inhibitors) when given acutely invariably inhibit the muricidal response of the rat This inhibitory effect is sufficiently well established that the suppression of muricide has been widely used as a prospective screening technique for the initial identification of potentially useful thymoleptic agents (Horovitz 1965 1966 Leaf et al 1969 Horovitz and Leaf 1966 Sofia 1969a Ueki et al 1972 Kamei et al 1975 Malick 1976 Valzelli and Bernasconi 1976) and monoamine oxidase inhibitors (Sofia 1969b DiChiara et al 1971 Ueki et al 1972 Valzelli and Bernasconi 1976)

While the suppression of muricide by antidepressants is undeniable its relationship to either the mode of action of antidepressant drugs or more generally to CA function is open to question on several grounds To date no chronic tests of antidepressant effects upon muricide have been reported nevertheless a) antidepressants induce depression rather than relieve it when given acutely to humans (Oswald et al 1972) and b) a minimum of two weeks of administration is usually required prior to a clinically observable thymoleptic response in depressed patients Thus whatever the mechanism for the acute antimuricidal effects of antidepressants may be it may possibly be unrelated to the clinical course of action for antidepressant effects

Furthermore much recent evidence suggests that serotonin and not catecholamines may be involved in many of the therapeutic effects of antidepressant drugs (Carlson et al 1969a b) Dubinsky et al (1973) directly tested the proposition that the antipredatory effects of antidepressants were due to a blockade of serotonergic reuptake and their results strongly suggested that only drugs with serotonin potentiating activity reduced feline predatory attack In particular they reported a reversal of antipredatory effects of antidepressants with PCPA*

PCPA – P-chlorophenylalanine

which in turn was reversed by precursor loading On the other hand CA depletion was ineffective in modifying the antipredatory effects of tricyclic drugs Moreover chlorimipramine a 5HT reuptake inhibitor reduced predation while the NE active reuptake inhibitor desmethylimipramine did not This argues for 5HT involvement and against NE A similar involvement of 5HT has recently been reported in the muricide test (Franck 1972)

It should also be noted that other antidepressant treatments may not alter muricide or other forms of predation Rush and Mendels (1975) report that the antidepressant lithium was virtually without effect in the muricide test This has been confirmed by Mukherjee and Pradhan (1976) Similar negative findings have been reported with experimental antidepressants such as iprindole or LU3080 (Dubinsky and Goldberg 1971) Moreover while the elimination of rapid eye movement sleep (REM sleep) has been reported to be of therapeutic benefit in depression (Hartmann 1973) surgical disruption of the locus coeruleus the noradrenergic pontine nucleus that controls REM may actually increase aggressive behaviors including possibly predatory behavior (Jouvet 1975)

## Postsynaptic Agonists

Perhaps the most specific and direct means available of assuring increased postsynaptic receptor stimulation is to inject exogenous neurotransmitter directly into discrete CNS loci Thus manipulation has produced consistent albeit site-specific results For example it is clear that the amygdala contains adrenergic receptors which inhibit muricide Leaf et al (1969) report that muricide was disrupted in several strains of rat after tamping of NE into the medial and basolateral nuclei of the amygdala A number of CA precursors were also shown to inhibit muricide On the other hand injection of NE or E into most diencephalic sites from which predation was elicitable by other drugs produced at best slight inhibition and NE or E injections into many sites were in fact inert with respect to this behavior (Bandler 1969 1970a 1971) In marked contrast to both of these findings however mesencephalic injection of NA into or near the ventral tegmental area of Tsai induced and facilitated an irritable form of mouse killing (Bandler 1970b) This syndrome included all normal aspects of killing however rats were difficult to handle It would be of interest to know if the local application of blocking agents would produce effects converse to the above

We have also observed increases in predation after injection of NA into the third ventricle of the cat (Katz 1976a) The facilitating action of NE was approach-specific and terminal attack patterns appeared unchanged by drug treatment Since this facilitation of attack was approach-related it might represent either a direct effect upon the predatory circuit involved with approach or an indirect effect NA is known to increase locomotor and exploratory behavior

(Segal and Mandell 1970 Segal et al 1974 Stone and Mendlinger 1974) and such motor effects cannot be ruled out

A number of interpretations may be given to the present results On one hand it is quite possible to imagine two behaviorally opposed NA circuits involved in predatory attack Since three major NA systems have been identified (Jacobowitz 1973 Lindvall and Bjorklund 1974) there is no contradiction in ascribing both inhibitory and excitatory behavioral functions to different neural systems In fact there is at least some motivational precedent for this, since different NA systems influence feeding in a similar manner The ventral NA bundle inhibits feeding (Ahlskog and Hoebel 1973 Hoebel 1975) while the NA bundles associated with the medial tegmental radiations and possibly the $A_6$ nucleus may excite and facilitate the feeding response (Jacobowitz 1973 Leibowitz 1972 1975 Micco 1974 Ritter et al 1975 Stein 1975) At best only limited data are available correlating individual NA systems with attack however it might be noted that a pathway within the general area of the intermediate bundle showed degeneration after lesions of attack sites (Bandler and Flynn 1974) while lesions of the ventral NA system did not affect muricide (Hoebel personal communication)

Even within a given system however changes in behavior due to the administration of a postsynaptic agonist are often difficult to interpret and depending upon the nature of neurotransmitter involvement behavior may be either facilitated or inhibited by the same drugs at different dosages In the first place it is possible that postsynaptic stimulants may also have affected presynaptic autoreceptors i e receptors along the axon and cell body of a neuron that a) are sensitive (often differentially sensitive) to the same class of neurotransmitter that is released postsynaptically and b) are presumed to serve local feedback and pacemaker functions (Carlsson 1975) These autoreceptors have been shown to have inhibitory rather than excitatory behavioral actions For example DA stimulants have been shown to exert a biphasic dose response relation upon psychomotor activity depending upon the relative degree of occupation of pre and postsynaptic sites (Carlsson 1975)

Postsynaptic stimulation may also produce either inhibitory or excitatory effects depending upon the relationship between central stimulation and behavior Two models exist for synaptic behavioral interactions The most simple and straightforward relationship is the so-called respondent relationship (Stein 1975) In the respondent relationship postsynaptic occupation is a necessary and sufficient condition for the elicitation of behavior For example clonidine induces feeding by purely respondent occupation of receptors (Stein 1975) and it might be anticipated that other respondent behaviors should also be facilitated by postsynaptic agonists

On the other hand many behaviors are maintained by the specific CNS consequences of behavioral chains Voluntary or operant behaviors require not only

reward (i e a central neurochemical stimulation of reward receptors) but also a contingent relationship between behavior and reward Noncontingent receptor stimulation of operantly maintained behaviors may in fact be behaviorally dis rupting For example self stimulation that is noradrenergically mediated at least in part was facilitated by administration of exogenous neurotransmitter which possibly was taken up presynaptically and released upon contingent stimulation Nonetheless it was disrupted by the adrenergic agonist clonidine which had a postsynaptic action (Stein 1975) * Indeed we might ask why an animal should continue to perform a reinforcement-contingent behavior if the central reward mechanism is already fully activated Likewise presession injections of many addictive drugs (morphine cocaine and amphetamines) reduce normally main tained drug-seeking behaviors possibly also through postsynaptic effects (Weeks and Collins 1964 Pickens and Harris 1963)

Clearly predation has both respondent (Flynn 1967 1972) and operant (Roberts and Kiess 1966 Myer and White 1965 Van Hemel 1972) compo nents at a behavioral level and it is therefore difficult to predict whether respon dent elicitation or the disruption of operant contingency would be the predomi nant behavioral effect of synaptic occupation (Katz 1976a) The use of post synaptic agonists by themselves may therefore be an undesirable research strategy

## INTERFERENCE WITH SYNAPTIC TRANSMISSION

A second strategy for investigating predatory behaviors involves the admin i tration of agents that interfere with neurotransmission i.e postsynaptic blockers biosynthesis inhibitors and amine selective neurotoxins The present section reviews the contribution of each of these three techniques to our under standing of the role of CA in predatory aggression

### Effects of Postsynaptic Blockade

A variety of CA blockers such as the neuroleptic drugs chlorpromazine and haloperidol have been evaluated in the muricide test and it is clear that neuro leptics do in fact block the muricidal response It must be noted however that unlike thymoleptics psychostimulants and other classes of drugs that block muricide without interfering with alertness or motor control thus blockade is

One complication in the clonidine mediated reduction in reward again rests with its possibl. presynaptic action (Svensson et al 1975) Clearly since not all dosages affect both sets of receptors equally a dose-response curve (not supplied in the paper) would clarify the role of different receptor types.

not separable from the sedation and ataxia producing side effects of these drugs (Karli 1958 1959 Sofia 1969a Janssen et al 1962 Kamei et al 1975 Valzelli and Bernasconi 1976) Thus while neuroleptics depress predation they may be acting only indirectly upon a predatory substrate Nonsedating neuroleptics (e g sulpyrid) may decrease predation while having fewer effects upon motor activity (Valzelli and Bernasconi 1972) however their pharmacological mode of action may not be catecholaminergic

### Effects of CA Depletion

It is also possible to interfere with CA neurotransmission by the selective blockade of either tyrosine hydroxylase the rate limiting enzyme for all CA biosynthesis or by interfering specifically with dopamine b hydroxylase the synthesizing enzyme for NE and E The use of dopamine b hydroxylase inhibitors allows a specific examination of NA and E involvement since DA remains intact while other CA are depleted

Examples of NA depletors that have been used include disulfiram (Antabuse) (Goldstein and Nakajima 1967) and diethyldithiocarbamate (DEDTC) a metabolite of the latter Both disulfiram (MacDonnell and Fessock 1969 1972) and DEDTC (Katz 1976a) have been employed in the investigation of feline biting attack Both drugs decreased approach to the attack object at dosages that did not produce overt sedation and at least some DEDTC treated cats actually showed concomitant increases in affective display and defensive reactions upon the approach of the experimenter (Katz unpublished observations) Thus unlike neuroleptics biosynthesis inhibitors may decrease attack without interfering with alertness It should be noted that MacDonnell and Fessock (1972) report intact and possibly increased biting after disulfiram and we also have observed no loss in terminal attack behaviors after drug treatment Thus interference with NA biosynthesis produced deficits in attack which were specifically approach related This finding may have three possible interpretations 1) NA depletors interfered with predation 2) they altered a more general and approach related system or 3) the drugs affected an approach system that subserved some unique functions that were specific to attack Clearly testing with other goal stimuli might clarify this issue

### Effects of AMPT Upon Predation

Depletion of whole brain CA may be achieved by the tyrosine hydroxylase inhibitor alpha methyl paratyrosine (AMPT) While reports are conflicting four reports suggest that attack in both cats and rats is disrupted Katz and Thomas (1974) using a low (75 mg/kg) dosage of AMPT found a disruption of approach related components of prey attack in the cat similar to those reported for NA depletion As in previous reports terminal attack was relatively unaffected

McLain and Powell (1972) found a low dosage of drug (50 mg/kg 3 times) also disrupted attack in the rat This is consistent with earlier informal observations of Salama and Goldberg (1970) (no dosage reported) Finally Banerjee (1974) reported that 125 mg/kg (3 times) reduced predation although the relatively large dose may have produced nonspecific sedation

On the other hand Kayser and Leaf (1968) report sporadic increases in attack in a small percentage of non killing rats (200 mg/kg L-AMPT) and no change in the majority of injected subjects and McLain et al (1974) also report possible increases in muricide (50 mg/kg of AMPT for 3 days) It might be noted that both increases are difficult to evaluate given the statistical treatments employed Kayser and Leaf used a Fisher exact analysis although their data were not readily amenable to it (in fact the change was not significant if a t test is employed) and McLain et al (1974) did not present a separate statistical analysis of this effect Finally Banerjee (1974) reported that AMPT caused normally indifferent rats to be more reactive to mice however this reactivity was not accompanied by increased killing

## Effects of Amine Specific Lesions

Reis (1974) and Jimerson and Reis (1973) suggest that intrahypothalamic injection of the CA specific neurotoxin 6 hydroxydopamine (6 OHDA) disrupts prey killing in the rat A similar disruption of attack has been observed after intraventricular injection (Banerjee 1974) Descriptions of the attack patterns after drug injection suggest that they are qualitatively similar to those seen after [illegible] and AMPT i e approach aspects of attack are disrupted but terminal reflexes remain fundamentally intact Dubinsky et al (1973) reported that 6 OHDA also had attack disrupting effects in the cat While this report did not specify the behavioral characteristics of the disruption (i e approach or terminal response decrements) it is possible that this syndrome was also characterized by approach specific deficits (Dubinsky personal communication)

On the other hand initial predisposition to attack may affect drug outcome Banerjee (1974) reports that 6-OHDA may produce mock attack (sic) or muricide in normally indifferent rats This dependence upon initial predrug behavioral response is reminiscent of the effects of amphetamines and points to a possible systematic influence of initial rat-mouse social behavior upon later drug response

The results of both AMPT and 6-OHDA taken together may indicate the involvement of NA as a facilitatory neurotransmitter in predation This involvement appears to be approach related and thus may also indicate the existence of a chemically distinctive non-CA substrate for terminal behavior It might be noted that these reports on CA depletion when taken in conjunction with the results from NA stimulation of the amygdala may point to some degree of involvement of both behaviorally excitatory and inhibitory NA circuits in attack.

Moreover initial attack tendency may be an important variable in the relative predominance of excitation or inhibition

A final means of approaching the issue of CA effects upon predation involves the assessment of amine turnover in the brains of killing vs nonkilling rats of the same strain While such differences may represent a host of differences extrins. to the killing response itself (e g arousal general reactivity and possibly the presence of a linked gene) they may nonetheless be of interest and they may a.i in clarifying the possible roles of amines in attack especially when they are taken in conjunction with data from other approaches Goldberg and Salama (1969) and Salama and Goldberg (1970) have reported specific increases in fore brain NA turnover in the brains of muricidal rats Their testing and assay schedules involved an extended period between the initial testing of muricide and subsequent biochemical assay It is therefore unlikely that the arousal of killing per se or other differences that were related to the actual attack sequence affected the reported differences This same research group has recently reported additional evidence for increased forebrain NE turnover in muricidal rats (Salama and Goldberg 1973) There was a significantly greater increase in loco-motor activity in muricidal rats than in control rats after both groups were given amphetamines Biochemical measures were consistent with previous reports a d this was interpreted as a possibly greater CA postsynaptic sensitivity on the part of muricidal rats

These changes have been confirmed by other recent reports (Valzelli 1971) *and suggest a facilitatory role for NE in predation* While these appear to be the major neurochemical changes associated with spontaneous muricide it should b noted that a decrease in 5HT turnover may also occur in muricidal rats (Valzelli 1971 Valzelli and Bernasconi 1972)

One final point might be made about turnover measures They may not re-flect functional i e postsynaptic alterations One means of looking at post synaptic factors would be an examination of CA metabolites In general deami nated by products represent presynaptic mitochondrial oxidative processes while o methylated catechols are a result of postsynaptically located COMT* Thus o-methylated catechols may be the measure of choice

An adequate experimental description of the effects of a given neurotrans mitter upon predation must take account of the many possible methodologic and conceptual difficulties inherent in an experimental situation We see in the present results at least seven possible difficulties

1 Results often reflect idiosyncratic measurement not all measures of attack covary and drugs have been shown to act selectively within a given model Thus a relationship between a given drug and predatory syndrome may depend both upon drugs and the nature of the dependent behavioral variable Cl arly one means of approaching this problem is to measure a variety of behaviors within *each predatory episode*

*COMT – catechol-o methyl transferase

2 Behaviorally converse phenomena (i e induction and suppression of killing) may not be converse at a pharmacologic level We have seen that amphetamines can decrease muricide but increase killing in nonkillers This may reflect the complexity of drugs employed and the underlying complexity of the behaviors observed

3 Drugs may have biochemical side effects that are not initially appreciated and that may themselves affect predation e g amphetamines and antidepressants may potentiate both CA and serotonin Thus it is difficult to ascribe behavioral changes induced by these drugs uniquely to CA There is therefore a clear need to carry out pharmacologic controls for confounding side effects

4 Not only may attack measures vary within species but drugs may produce oppositely signed changes in different species and models of attack We might question in this regard whether behaviorally analogous predatory syndromes are necessarily also physiologically homologous

5 Drugs may affect attack through their effects upon alertness coordination or motor activity (tranquilizers may have these effects)

6 A biochemically unambiguous event may produce behavioral changes that are difficult to interpret e g postsynaptic excitation may increase or decrease behavior depending upon the operant or respondent contingencies that maintain it

7 The same neurotransmitter may be involved in different and possibly opponent neural systems which subserve differing behavioral functions

While no simple or straightforward relationship has been unequivocably demonstrated for neurotransmitters and predation at least some evidence — based on the one hand upon local injections in the amygdala and possibly the effects of psychostimulants and on the other hand upon more caudal injections the effects of synthesis inhibition and endogenous turnover differences — speaks of the possibility of both excitatory and inhibitory influences upon predation at least for NE As yet little at all can be said about the possible involvement of DA or E however they too may play as yet unspecified roles In general the possibility of a unique epinephrine mediated role in predation has received only scant attention to date Yet epinephrine is localized in the CNS (Hokfelt et al 1974) and many of the hindbrain cell bodies from which attack may be elicited (Berntson 1973) are located in or near these adrenergic nuclei and fiber bundles

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AGGRESSIVE BEHAVIOR
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# Social Aggression and Power Relations Among Preschool Children

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Social agonism and dominance relations were assessed in two preschool groups. An average of 30 hours of observational data was obtained for each group during free play over a six week period A Social Agonism Inventory describing specific initiation and response behaviors during episodes of social conflict was used to code agonistic activity Dyadic interactions were examined to determine whether the resolution of agonistic interactions conformed to a linear model of social dominance Although there were group differences in the relative frequency of different forms of conflict systematic comparison of agonistic wins and losses revealed similarly rigid and linear dominance structures at both preschools The relation of aggression and dominance was empirically examined by comparing the initiation and receipt of agonism by high vs low dominance status children Higher dominance status children engaged in more agonistic interactions but a majority of these interactions were directed toward other high ranking group members.

Key words agonistic interaction dominance hierarchies, naturalistic observation, peer group conflict preschool behavior power relations, social aggression social status

Within the nonhuman primate literature the analysis of social power has been operationalized as the relative ability to terminate favorably episodes of social conflict An animal which ends an aggressive interaction by engaging in submissive behavior is viewed as having less social power than this more dominant competitor Social dominance has been viewed as a basic dimension of primate social organization and it has been related to a number of social processes such as group defense [Jolly 1972] social learning [Strayer 1976] subcultural developments [Tsumori 1967] and the nature of free play [Dolhinow and Bishop 1972] Theoretically the formation and maintenance of a stable domi

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nance hierarchy functions to minimize intragroup aggression by permitting ritualized expressions of power relations within the group Dominance defines specific social prerogatives of each group member in each possible dyadic social context

Early primate researchers often attempted to assess social dominance in terms of a single type of interaction Usually such interactions consisted of artificial competitions in a controlled setting Such indices were eventually shown to be inadequate since they failed to generalize to other more natural social settings [Bernstein 1970] In more recent research and in our work with young children dominance has been reserved as a *general descriptive* concept that summarizes stable social relationships evident during the resolution of various forms of naturally occurring conflict [Bernstein 1970 Hinde 1974 McGrew 1972 Strayer and Strayer 1976] Used in this way dominance reflects the asymmetrical nature of power relations within pairs of individuals who comprise a social group The organization of all such dyadic relations reflects the power structure or dominance hierarchy for the social group In dyadic dominance one member of a social pair regularly submits to the other A measure of the degree of such asymmetry in bouts of dyadic conflict provides an index of rigidity in dominance relations for the group Primate power structures are usually governed by a linear transitivity rule Thus in most dominance hierarchies if A dominates B and B dominates C then A also dominates C A measure of the exceptions to this linear rule provides an index of the extent to which a linear dominance model accurately describes the power structure for a social unit

The concept of social dominance provides a good bridge linking ethological and psychological approaches to behavioral research Dominance is a structural concept describing an organizational aspect of social relationships and social groups For an ethologist the concept of dominance has meaning only in relation to the group and is best viewed as an emergent property of a group at the structural level of analysis Psychologists have tended to focus on both aggression and dominance as individual descriptors or trait concepts ignoring the possible functions and organization of aggression within the social group The present paper combines these two approaches in the examination of social conflict in two groups of young children From a psychological perspective emphasis is placed on individual differences in the initiation and termination of conflict episodes From the ethological perspective the analysis of such interactions provides an objective index of dyadic dominance relations which ultimately permits the derivation of a power structure for each group

In order to determine the applicability of the above model of dominance to young children s peer groups two preschool groups of children between the ages of 3 and 5 years were observed Each group was observed daily for six weeks [illegible] play The first group of 17 children was observed at the [illegible] Center in Vancouver *British Columbia* Canada and the

second group of 19 children was observed at the Early Childhood Education Centre at the University of Waterloo in Ontario Canada

Systematic observations were obtained from videorecords of naturally occurring conflicts Two half hour samples were collected each day Data were obtained usin a matrix completion method This method attempts to obtain data on as many dyads as possible in order to provide representative behavioral episodes for each dyad rather than to estimate actual rates of conflict [Altmann 1974] All episodes of social agonism were scored in four item statements Each statement identified the initiator the target child the pattern of initiated agonism and the response of the target If an episode consisted of an extended sequence includ ng a number of counterattacks each act was scored separately

The determination of social dominance rested on the identification of specific behaviors describing the initiation and termination of conflict episodes The general categories of naturally occurring social conflict and the specific action patterns that describe them are fully elaborated in Strayer and Strayer [1976] A summary of the descriptive categories is shown in Table I In particular sub mission responses to attacks and threats have been shown to provide the best fit for dominance relations among both primates and children Struggles over objects and space have also been u ed to index dominance relations The use of object/ position struggles differs somewhat from the order based on attacks and threats principally because the loss or perhaps abandonment of an object is not the same as a *submissive* response

The importance of submissive responses in defining group dominance structure was pointed out by Rowell [1966] in nonhuman primate work and it is evident in our work with children as well as illustrated by Tables II and III Table II presents a matrix of all agonistic interactions observed for a group of preschool children *regardless of the target s response* There is nothing like a hierarchical structure evident here In contrast Tables III and IV show a matrix of classes of aggression that led to a submissive response Table III clearly shows a linear dominance hierarchy for the Langara group and Table IV shows a similar hierarchy for the Waterloo group The entries below the diagonal indicate episodes in which the linearity of dominance was violated Linearity refers to the degree to which observed dyadic relations fit the prediction implicit in the model of linear dominance hierarchies In Tables III and IV two dyadic predictions in each sample were not predicted by the model and are marked by an asterisk Rigidity refers to the number of episodes in which a less dominant child never theless won in a minority of interactions as illustrated by PE in Table III and by A in Table IV A comparison of the linearity and rigidity of the dominance hierarchies observed in these two groups of children with a dominance hierarchy observed in a troop of captive macaque monkeys (Strayer 1976) is shown in Table V It is clear that at a structural level the dominance hierarchies among these groups of young children are nearly as linear and rigid as those observed

TABLE I Categories of Social Agonism

| Initiated behaviors | Response behaviors |
|---|---|
| Physical attack | Submission |
| Chase | Help-seeking |
| Push pull | Cry scream |
| Hit | Rapid flight |
| Kick | Cringe |
| Bite | Hand-cover |
| Wrestle | Flinch |
| | Withdrawal |
| Threat gestures | Counter |
| Face and body posture | |
| Intention hit | |
| Intention kick | |
| Intention bite | |
| Object/position conflict | No response |
| Object struggle | |
| Supplant | |

within the group of nonhuman primates

The relative frequency of various classes of agonistic activity among preschool children is shown in Table VI The distribution is fairly similar across both groups except for the higher proportion of object/position struggles and counters (primarily relating to objects) for the Waterloo group This finding may refle the effects of setting since the children of Waterloo were observed durin winter in an indoor setting with spatial constraints and many toy related play activit es. Such environmental factors may influence the form of social conflict in a sta group in a fashion roughly analogous to the effects of artificial provisioning on competition and aggression in feral troops of nonhuman primates

It is clear that agonistic interactions among preschoolers are organized in terms of a group dominance structure The function or social benefit of such structuring has been considered to be the resulting constraint of total aggression within the group In an attempt to explore the relation of dominance status and aggression the distribution of total agonism as a function of dominanc status was examined Table VII shows the percentage of agonism directed towards and received by high and low status individuals in the group High or low status assignments were made using a median split to divide each group Among macaque monkeys [Strayer 1976] it is clearly the high-dominant animals who initiate the majority of agonistic interactions Their aggressive behavior is distrib- uted equally across high and low status group members For children the picture is somewhat different High status group members confined the majority of their aggression to other high ranking children And although low ranking members of the group received nearly half of the total aggressive actions they

TABLE II Total Agonism Observed at Langara

| Social initiators | Social targets RO | SS | BR | IF | TD | SD | PE | IR | CS | KA | CH | TY | GL | SA | ME | JU | SH | Total initiated |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RO | xx | 1 | 3 | 4 | 1 | | | 1 | 1 | | 1 | | 7 | | 1 | | | 20 |
| SS | 1 | xx | 7 | 8 | 2 | 1 | 1 | 12 | 3 | | 1 | 1 | 4 | 1 | | | 2 | 44 |
| BR | 1 | 4 | xx | 7 | 3 | 2 | 2 | | 1 | | 8 | 1 | 5 | 5 | | | 1 | 40 |
| IF | 3 | 3 | 2 | xx | 3 | 1 | 13 | 3 | 5 | 1 | | | 8 | 3 | | 2 | 1 | 48 |
| TD | 1 | | | 3 | xx | 4 | 6 | | 8 | 5 | 1 | | 1 | 3 | | 2 | 1 | 35 |
| SD | | | | | | xx | 2 | 8 | 11 | | 4 | | 4 | 3 | | 1 | | 35 |
| PE | 1 | | 1 | 9 | 3 | 4 | xx | 2 | | | 1 | | 7 | 9 | 1 | 1 | | 39 |
| IR | | | | 1 | 1 | 1 | 2 | xx | 7 | 5 | 1 | 1 | 1 | | | | | 20 |
| CS | 1 | 1 | 1 | 2 | 5 | 11 | | 3 | xx | | | | 1 | | | | | 25 |
| KA | | | | | | | 1 | | | xx | | 11 | | 1 | | 1 | 4 | 18 |
| CH | 4 | | 4 | 3 | 3 | 2 | 1 | | | | xx | 3 | 11 | 5 | | 2 | 2 | 40 |
| TY | | | | | | | | | | 2 | | xx | 2 | | 8 | | | 12 |
| GL | | 1 | 9 | 3 | | 3 | 6 | | | | 11 | 2 | xx | 1 | | 7 | 5 | 48 |
| SA | | 1 | 4 | | 1 | 2 | 1 | | | | 1 | | 1 | xx | | | | 11 |
| ME | | | | | | | | | | | | 3 | | | xx | | | 3 |
| JU | | | | | | 1 | | | | | | 1 | 1 | | | xx | | 3 |
| SH | | | | | | | | | 1 | 1 | | | | | | | xx | 2 |
| Total received | 12 | 11 | 31 | 40 | 22 | 32 | 36 | 30 | 37 | 14 | 29 | 23 | 53 | 32 | 9 | 16 | 16 | 443 |

TABLE III Langara Dominance Structure*

| Social initiators | Social targets RO | SS | BR | IF | TD | SD | PE | IR | CS | KA | CH | TY | GL | SA | ME | JU | SH | Total initiated |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RO | xx | 1 | 1 | | 1 = | | | | | | | | 1 | 1 | | | | 5 |
| SS | | xx | 1 = | 3 | 1 | | | 4 | 1 | | | 1 | 3 | | | | 1 | 15 |
| BR | | 1 = | xx | 1 | 1 | | | | 1 | | 6 | | 3 | 2 | | | 1 | 16 |
| IF | | | | xx | 2 | 1 | 8 | 2 | 2 | 1 | a | | 4 | 2 | | 2 | 1 | 25 |
| TD | 1 = | | | | xx | = | 3 | | 7 | 2 | | | | | | | 1 | 14 |
| SD | | | | | = | xx | 1 | 1 | 4 | 2 | 1 | | | a | | 1 | | 10 |
| PE | | | | | 1 | | xx | 1 | | | | | 1 = | 3 | | | | 6 |
| IR | | | | | | | | xx | 3 | 2 | 1 | | | | | | | 6 |
| CS | | | | | | 2 | | 1 | xx | = | = | | 1 | | | | | 4 |
| KA | | | | | | | | | = | xx | = | 9 | | 1 | 1 | 1 | 3 | 14 |
| CH | | | | 1a | | | | | = | = | xx | = | 5 | 3 | | 1 | 1 | 11 |
| TY | | | | | | | | | | | = | xx | 1 = | = | 2 | | | 3 |
| GL | | | | | | | 1 = | | | | 1 | 1 = | xx | = | = | 3 | 5 | 11 |
| SA | | | | | | 1a | | | | | 1 | = | = | xx | = | | | 2 |
| ME | | | | | | | | | | | | | | | xx | = | = | 0 |
| JU | | | | | | | | | | | | | | | = | xx | = | 0 |
| SH | | | | | | | | | | | | | | | = | = | xx | 0 |
| Total received | 1 | 2 | 2 | 5 | 6 | 4 | 13 | 9 | 18 | 7 | 10 | 11 | 19 | 12 | 2 | 9 | 12 | 142 |

An equals sign indicates tied dyadic relation
[a]Indicates reversal of linear dominance

TABLE IV Waterloo Dominance Structure[a]

| Social initiators | Social targets | | | | | | | | | | | | | | | | | | | Total initiated |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MA | CH | JA | BL | TL | JO | CM | JE | EL | EF | BK | EM | EH | PA | RS | RM | SH | BP | CA | |
| MA | xx | = | 2 | | | 1 | | 2 | 1 | | | | 1 | | 1 | | 1 | | | 9 |
| CH | = | xx | 10 | 2 | 1 = | 1 | 1 | 8 | | 1 | | | 1 | | 1 | | a | | | 26 |
| JA | | 1 | xx | 4 | 2 | 2 | 1 | 3 | | 2 | | | 10 | | | | | | | 25 |
| BL | | | 1 | xx | 1 = | 1 | 1= | | | | | | | | | 1 | | | | 5 |
| TL | | 1= | 1 | 1= | xx | 1 | | 5 | 2 | 8 | 2 | | 3 | 1 | | 3 | | 1 | 2 | 31 |
| JO | | | 1 | | | xx | 1 | | | 2 | | | 1 | | | | | | | 5 |
| CM | | | | 1= | | | xx | = | = | 1 | | | 1 | | 1 | | | | | 4 |
| JE | | | 1 | | | | = | xx | = | 2 | 2 | | 2 | | | | | | | 7 |
| EL | | | | | | | = | = | xx | | 1 | | | | | | | | | 1 |
| EF | | | | | 1 | 1 | | | | xx | 1 | 1= | | | | | | 1 | | 5 |
| BK | | | | | | | | | | | xx | 3 | 1 | | | | | 1 | | 5 |
| EM | | | | | | | | | | 1= | | xx | = | | | | | | | 1 |
| EH | | | | | 1 | | | | | | | = | xx | 1 | | | | | | 2 |
| PA | | | | | 1 | | | | | | | | | xx | 1 | | | 2 | | 3 |
| RS | | | | | | | | | | | | | | | xx | 1 | a | | | 1 |
| RM | | | | | | | | | | | | | | | | xx | 1 | | | 1 |
| SH | | 1[a] | | | | | | | | | | | | | 1[a] | | xx | = | 1 | 3 |
| BP | | | | | | | | | | | | | | | | | = | xx | = | 0 |
| CA | | | | | | | | | | | | | | | | | | = | xx | 0 |
| Total received | 0 | 3 | 16 | 8 | 6 | 7 | 4 | 18 | 3 | 17 | 5 | 5 | 20 | 2 | 5 | 5 | 2 | 5 | 3 | 134 |

[a]An equal sign indicates tied dyadic relation
[a]Indicates reversal of linear dominance

**TABLE V Comparison of Dominance Hierarchies**

| Group | Linearity (%) | Rigidity (%) |
|---|---|---|
| Macaque monkeys | 100 | 90 |
| Langara | 98 | 97 |
| Waterloo | 96 | 94 |

**TABLE VI Relative Frequency (%) of Agonistic Activity**

| Category | Langara | Waterloo |
|---|---|---|
| Initiations | | |
| Physical attacks | 39 | 18 |
| Threat gestures | 33 | 20 |
| Object/position struggles | 28 | 62 |
| Responses | | |
| Help seeking | 1 | 1 |
| Submission | 39 | 28 |
| No response | 39 | 27 |
| Counter | 21 | 43 |

**TABLE VII Distribution (%) of Agonism as a Function of Status Position***

| Group | H→H | H→L | L→H | L→L |
|---|---|---|---|---|
| Macaque monkeys | 46 | 45 | 0 | 9 |
| Langara | 46 | 28 | 13 | 13 |
| Waterloo | 55 | 19 | 13 | 14 |

*H) High status L) low status

also initiated considerably more agonistic episodes with high status children Thus there seems to be more balance in the distribution of aggressive behavior among preschool children than among members of the stable primate group

Finally in discussing the concept of dominance in relation to that of aggression, it is important to note that in both preschool groups the most aggressive children (ie those who initiated the most aggressive actions) were not necessarily the most dominant The status rankings of the most aggressive children ranged from 4 to 14 Similarly the children who were most often the target of social aggression were not necessarily the lowest ranking in their group In both cases it would be misleading to assume that there is a necessary correspondence between a child s tendencies to engage in aggressive and submissive behaviors and his ultimate position within the group power structure

In conclusion the distinction between social dominance and the individual traits of aggressiveness and submissiveness seems necessary for a more adequate analysis of young children s social conflict Such a distinction permits an empirical specification of the possible relations between rates of specific activities (which may provide an objective index of personality traits) and the social context where these activities naturally occur An ethological analysis of the organization of naturally occurring aggressive behavior seems to provide critical information on the social ecology of the peer group and the individual child s role within the social unit Undoubtedly an adequate appreciation of the incidence and diversity of either aggressive or submissive behaviors must include some consideration of the natural social constraints on these activities which are imposed by the nature of a child s social relationships with his peers

Finally it seems important to stress that the analysis of social power is but one aspect of peer group social ecology Conflict and aggression do not describe a major portion of young children s social behavior But the analysis of agonistic activity provides an objective behavioral index of group power relations Apparently such power relations operate as a reliable and well formulated aspect of the group s social organization The extent to which other social activities such as affiliative overtures altruistic gestures leadership attention or even type of play may depend upon or be coordinated with the emergence and stabilization of dominance relations is an important consideration in both comparative and developmental analys s of social organization in stable groups Such questions suggest the need for a more elaborate descriptive analysis of these latter social activities that would parallel the ethological analysis of social power relations It seems important to stress that such research should carefully attempt to isolate action patterns that characterize these later activities and at the same time be aware of the various levels of organization that may appear in naturally occurring social behavior Perhaps in a fashion similar to that demonstrated for social conflict the dyadic context may be an important and powerful influence on an individual s likelihood to initiate and terminate these other types of social interactions

## ACKNOWLEDGMENTS

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# The Perception of Preschool Social Dominance

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Children s and teachers perception of social dominance was examined using a behavioral criterion for determining accuracy of verbal judgments. Video records of agonistic interactions were obtained during approximately 60 hours of free-play at two preschool centers. Analyses of social conflict episodes ending in submission revealed linear dominance structures for both groups. Dominance perception was assessed in two ways Both teachers and children were asked to rank-order a subgroup of children according to dominance They were also asked to select the more dominant children in a number of predetermined pairs. Results indicated that teachers could accurately judge dyadic dominance relations and that accuracy among children varied as a function of their status within the group hierarchy Findings have implications for social dominance assessment methodology and for the issue of consensual versus ecological validity in developmental studies of social perception.

Key words. social perception ecological validity aggression agonism dominance hierarchy naturalistic observation

## NTRODUCTION

It is only during the past five years that both concepts and methods from animal social ethology have been applied directly to the study of human social nteraction Most of these studies have focused upon preschool behavior and

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particularly upon preschool social dominance Two quite different approaches have been used to investigate social dominance among young children A number of researchers have examined naturally occurring episodes of social conflict in order to determine dominance relations and status structures within stable peer groups Abramovitch [1976] and McGrew [1972] both found nearly linear status structures using wins during object conflict as a criterion for assessing social dominance Similar dominance hierarchies have been described by Misshakian [1976] and Strayer and Strayer [1976] who examined all social exchanges involving attack and submission A second approach to dominance assessment relies upon analysis of consensual agreements in children s verbal reports concerning dominance relations within their group [Omark Omark and Edelman 1975] According to the latter method when both members of a dyad agree concerning who is tougher the two children are considered to have an established dominance relationship All such established relationships are examined to determine the group dominance hierarchy

Although both approaches to the assessment of dominance have led to the identification of linear status structures for young children s peer groups potential discrepancies between the two procedures pose an important methodological question To what extent do the two procedures provide convergent information about the same structural aspects of the peer-group? A second and perhaps more psychologically interesting question concerns individual differences in agreement between statements concerning social relationships and a behavioral assessment of social interaction within the peer group

At a methodological level there are a number of potential problems inherent in use of the verbal report for the assessment of dominance relations It is conceivable that child A could overrate his dominance in relation to child B while the latter could underrate has dominance in relation to child A Using the verbal report method the dominance relation for this dyad would be considered consensually established by dyadic agreement This would result in unavoidable mistakes in the derivation of group dominance structure because there is no way of independently assessing instances of reciprocal errors A second problem occurs particularly in developmental research using verbal reports Since the derivation of a social dominance structure depends upon verbal agreement between a number of dyads within the group it is impossible to derive a hierarchy if there is insufficient or only chance agreement In the past it has often been difficult to derive social dominance hierarchies from verbal reports by preschool or nursery school children [Omark Omark and Elelman 1975]

Even when the verbal report method is used primarily to assess the accuracy of children s perceptions about dominance relations problems concerning the adequacy of the criterion for accuracy must be resolved If accuracy is judged in terms of verbal consensus alone it seems necessary at least to know how the consensual status structure obtained from children s reports compares with an

independent assessment from teachers or adult supervisors of the peer group Perhaps the most important question given the divergence of methods for the assessment of social dominance is how well verbal reports from both children and teachers reflect the group dominance relations derived from behavioral observation of intragroup conflict

The present investigation was designed to determine the extent of agreement between the verbal consensus and the behavioral assessment procedures Our primary interest concerned the degree to which preschool children and teachers were accurate in their perception of dominance relations and if children s accuracy of perception was related to their position in the social dominance hierarchy To answer these questions data from both behavioral and verbal report methods were compared

## BEHAVIORAL ASSESSMENT OF SOCIAL DOMINANCE

### Method

Two groups of preschool children were observed Only children who were present for at least 75% of the sampling period were included in the present analysis The first group attended the Langara City College preschool in Vancouver British Columbia This group included 17 children (seven girls ten boys) whose mean age was 53 4 months (SD = 7 6) The second group was observed at the University of Waterloo Early Childhood Education Centre in Waterloo Ontario This sample contained 18 children (ten girls eight boys) whose mean age was 51 4 months (SD = 7 1)

A total of 30 hours of videotaped social interaction was obtained during free play periods for each of the groups Records were collected daily for six weeks using a matrix completion sampling method [Altmann 1974] Episodes of conflict were analyzed using the behavioral inventory for preschool agonism reported by Strayer and Strayer [1976 1978] In each agonistic episode the initiator the initiating action pattern the target child, and the target s response were identified Social dominance hierarchies were constructed on the basis of aggressive interactions which terminated with a submissive response by one of the children involved in the dyadic exchange

### Results

Comparison of observations for the two groups showed that while most of the specific patterns of initiated agonism were present at both locations there were important differences between the groups in the relative frequencies of different forms of conflict Children in the Waterloo group were involved in two times more Object/Position struggles than children in the Langara sample The difference seemed attributable to differences between the two observational

settings While the Langara children were observed for the most part in an open playground the Waterloo study was conducted inside a university preschool center equipped with many toys and recreational materials The larger number of toys and the relatively closer proximity of other children may have contributed significantly to group differences in the frequency of Object/Position conflict A comparison of responses to initiated agonism indicated that although submissive patterns occurred with about the same relative frequency in both groups the children at Waterloo responded to agonistic initiations by counter attacking much more often At Waterloo 43% of responses were coded as counterattacks while at Langara there were only 23% ($\chi^2 = 11.90$ $p < 0.01$) Again this difference may reflect situational factors which regulate the nature of social conflict

Since our coding procedures identified both the initiator and target for each dyadic exchange conflict data could be analyzed in terms of the dyadic direction of social interaction These dyadic analyses were designed to evaluate the linearity and rigidity of social dominance relations (for a detailed report of these analytic procedures see Strayer and Strayer [1977]) Linearity of dominance represents the degree to which the rank ordering of individuals in a group conforms to the rule of transitivity that is if $A > B$ and $B > C$ then $A > C$ In both groups only two dyadic relations violated this rule thus the observed dominance structures were 98% and 96% linear The frequency of episodic reversals in typical agressor submittor roles within a dyad provides an indication of the rigidity of dyadic dominance relations For both samples the rigidity indices were quite high since more than 90% of social agonism was unidirectional within all dyads Thus *despite the differences in the relative frequency of various forms of* agonistic activity surprisingly similar dominance hierarchies were evident in the two preschool samples

## THE PERCEPTION OF DOMINANCE RELATIONS

### Method

At the close of the six week observational period both children and teachers at each center were invited to participate in an individual interview designed to assess their perceptions concerning dominance relations within the preschool group Fourteen children and three teachers were present for interviews at Langara 15 children and three teachers were present at Waterloo Two different approaches were used to assess the perception of social dominance

The first approach was designed to assess accuracy of dominance judgments in dyadic comparisons of peer group members There were two versions of this procedure, an other-other comparison in which the subject was not included in the stimulus pair and a self-other comparison in which the subject was one member

of the stimulus pair During each testing session the subject was presented with from 10 to 16 stimulus pairs and asked to select the tougher child in each pair Eight stimulus pairs were presented in the self other comparison to children at both preschools Individual photographs of peers were used during testing of children in order to prevent confusion about which classmates were being compared. In addition children were asked to give another word for tougher prior to testing in order to insure that they understood the term Since some children did not respond to all stimulus pairs a percentage correct score was obtained for each subject by dividing the number of correct responses by the total number of judgements made

The second approach to assessing the perception of social dominance emphasized judgments concerning children s position in the dominance hierarchy Teachers at both preschools were given a list of children s names and asked to order the entire group according to toughness Since in preliminary work preschool children had difficulty in rank-ordering a large group the subjects from the Lanzara sample were asked only to rank-order a subgroup of nine children (eight randomly selected classmates and themselves) This simpler task still proved quite difficult Consequently children at Waterloo were shown photographs of all children in the group including themselves They were asked to pick the child who was the most tough Their first choice was then eliminated and the question repeated yielding their second and third ranked classmates A composite score was given to each child based on the number of times each was ranked first second or third yielding a consensus rank score for 16 children in the Waterloo sample

## Results

Perception of dyadic dominance Since eight self-other comparisons were presented to children from each group it was possible to compare reciprocal judgments concerning relative dominance for 28 dyads in each sample At Lanzara 14 of these pairs of children agreed that one member of the dyad was tougher at Waterloo 16 pairs agreed Thus using the method of Omark Omark and Edelman [1975] there was 50% and 57% agreement on verbal reports of dyadic dominance Although these figures are slightly higher than the level previously reported for preschool children they confirmed the earlier finding that preschoolers agreement on dyadic dominance differs little from the percentage expected given random choices Consequently as in the earlier study [Omark Omark and Edelman 1975] it was not possible to construct a consensual status ranking based upon verbally established relationships which could be used to assess preschooler s accuracy of dominance perceptions

However accuracy of dyadic dominance judgments could be assessed relative to the behavioral observations To facilitate these comparisons children from both groups were calssified into High Medium and Low dominance categories

on the basis of their ranking in the behavioral dominance structure For the Waterloo sample five children were assigned to each status level For the Langara sample five children were assigned to the High and Low status groups and four to the Medium Figure 1 represents the mean accuracy of both children and teachers in these dyadic comparisons Inspection of other-other comparisons in both the Langara and the Waterloo samples shows that High and Medium status children are more accurate than the Low status group but not as accurate as the teachers A two way analysis of variance in accuracy on other-other comparisons

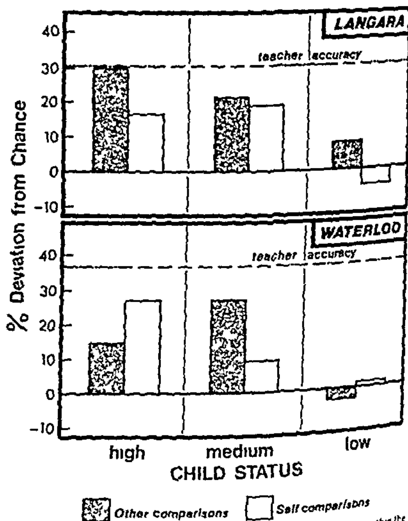



Fig 1 Accuracy of dyadic dominance judgments as a function of position within the dominance hierarchy

s a function of preschool group and status level indicated a significant main ffect only for status ($F(2\ 23) = 6\ 64$ $P < 0\ 01$) Figure 1 also shows that ıean accuracy in self-other comparisons appears to be related to the child s :atus position However statistical analysis indicated that there was considerable ariation in these latter accuracy scores within each of the status levels and that ie differences between levels was not statistically significant Mean accuracies or the three subgroups in self-other comparisons reflects the effects of both nder and overrating of their own dominance by some children in each status ubgroup

Perception of group status rankings Although the children s dyadic com arisons did not produce sufficient agreement to generate a single status ranking rom verbal reports for either group the results from the rank-ordering procedures rovided information which permitted rank-ordering of a subgroup of children n each sample By weighting individual scores given to each member in these ubgroups we were able to derive a single status ranking which reflected the eneral relative position assigned to the children by their peers Table I shows the legree of association between the status ranking obtained from children s and eachers verbal reports and the behavioral observations While it is clear that the eachers verbal reports (especially at Waterloo) agreed to a significant extent vith the behavioral assessment of the dominance structure the children s reports ppear much more discrepant Even if one takes into account the cognitive dif iculties inherent in the task of rank-ordering a group and uses the teacher s score is a ceiling the children s accuracy in both samples was at most marginal Their udgments provided the poorest consensual index of behavioral dominance rank ng for both groups Although teachers proved to be better judges of observed status ranking it should be emphasized that even the adult judgments provide

**TABLE I Rank Order Correlations Between Status Rankings Based on Behavioral Observations and Verbal Reports**

| | Type of dominance assessment | | |
|---|---|---|---|
| | Behavioral observations | Teachers reports | Children s reports |
| Langara (N = 8) | — | — | — |
| Teachers reports | 0 66* | — | — |
| Children s reports | 0 52 | 0 69* | — |
| Waterloo (N = 16) | | | |
| Teachers reports | 0 81** | — | |
| Children s reports | 0 51* | 0 44* | — |

* $p < 0\ 05$
** $p < 0\ 01$

on the basis of their ranking in the behavioral dominance structure For the Waterloo sample five children were assigned to each status level For the Langara sample five children were assigned to the High and Low status groups and four to the Medium Figure 1 represents the mean accuracy of both children and teachers in these dyadic comparisons Inspection of other-other comparisons in both the Langara and the Waterloo samples shows that High and Medium status children are more accurate than the Low status group but not as accurate as the teachers A two way analysis of variance in accuracy on other-other comparisons

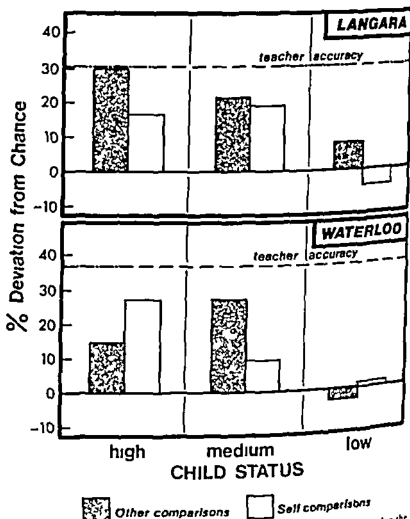



Fig 1 Accuracy of dyadic dominance judgments as a function of position within the dominance hierarchy

sponse bias Since higher status children approached the accuracy level of achers in other-other comparisons the latter interpretation of errors in self ther comparisons seems more plausible A profitable direction for future re arch would entail simultaneously examining social status perspective taking ias and accuracy of dominance perception

The extent to which people agree in their perception of social relations is an sue which is of interest aside from the question of whether or not they are rrect in their agreement As reported earlier by Omark Omark and Edelman 975] preschool children did not agree in dominance comparisons of them ves and classmates Furthermore their verbal reports differed from those of ichers in the preschool Children often gave idiosyncratic reasons for choosing e member of a dyad as tougher (eg He s tougher cause he s my friend or he s tougher she bites! ") The particular behaviors to which teachers and ildren selectively attend in order to judge social dominance remain to be in iated However since verbal interviews alone provide a relatively poor index actual dominance relations future research should include some form of uralistic behavioral assessment The strongest conclusion from the present earch is that behavioral observations provide a more complete picture of peer up relations Consequently in future research such observations should be d to assess development in social perceptiveness

## KNOWLEDGMENTS

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# A Guide to the Literature on Aggressive Behavior

Articles relating to the general problem area of aggression are scattered throughout the whole range of specialized journals in fields from A for anatomy to Z for Zoology It is virtually impossible for a single individual to find all the articles which may bear on his particular interest Information overload is of course a problem However an even greater problem is matching the interesting article with the interested reader Aggressive Behavior will attempt to alleviate this problem by publishing a list of references in each issue The reference list will be compiled from several sources Each article listed in Psychological Abstracts and indexed under the following terms will be included

1 Aggressive Behavior
2 Anger
3 Animal Aggressive Behavior
4 Attack Behavior
5 Hostility
6 Threat Postures
7 Violence
8 Frustration
9 Conflict

Each reference will be coded according to the index terms listed above and will be listed in alphabetical order by senior author There are a large number of journals that publish articles related to aggression that are not covered by Psychological Abstracts In order to find such references the cooperation of all readers of this journal is needed If each of the several hundred investigators concerned with the problem of aggression makes a habit of contributing to the literature search section of Aggressive Behavior the search task of each of us will be made easier If in your coverage of the literature you find an article about aggression in a journal that is not regularly abstracted by Psychological Abstracts put the full reference on a 3 X 5 card and send it to the editor for inclusion in this section

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AGGRESSIVE BEHAVIOR
Volume 4 pages 201–206

# Comparison of Agonistic Behavior in Individually-Housed Male Mice With Those Cohabiting With Females

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Videotape recordings of male mice group-housed individually-housed and cohabiting with females, were rated for their agonistic behavior in a "standard opponent" test. Previously mated male mice showed more fighting than isolated or grouped males. Marked differences in other social and non-social behaviors, which could not be accounted for in terms of increased fighting were not evident. These results suggest that agonistic behavior may be usefully studied by examining male mice that have cohabited with females. One obvious advantage is that such mice cannot be dismissed as being "socially deprived," as is sometimes claimed for individually housed mice Other advantages are that aggressiveness is induced quickly at high levels, and the mice appear very sensitive to hormone manipulation following castration

Key words aggression cohabitation with females, grouped isolate male mice videotape

## INTRODUCTION

Individually housed male laboratory mice seem to show behavioral responses that are similar to those evidenced by dominant/territorial males For example they readily attack a male conspecific that is introduced into their home or neutral cage [Brain and Benton 1977] Consequently these animals have proved popular

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in studies on the physiology underlying aggression as well as in screening drugs One criticism that has often been levelled at the use of isolated male mi e to generate fighting behavior is that they may be stressed by 'social deprivatio It is argued that they consequently show increased irritability [Cairns 197' Goldsmith et al 1976], which generates the fighting

It has recently been found that male mice that have been previousl ca ed with females show greatly elevated levels of fighting when introduced into the experimental cage with a standard opponent" [Brain and Bowden 1978] The standard opponent test is one in which an animal that is vi tually certain to be subordinate is used as a stimulus for attack [Brain & Poole 1974]

Mice rendered aggressive by cohabitation have been us d in a number of studies [Goyens and Noirot 1974 Brain and Poole 1976 Brain and Bowden 1978] They seem to have the advantage that they are very sensitive to the effects of steroid hormones administered after castration However their actual behav al pattern has never been analysed in detail to determine whether such animals show subtle differences in quality as well as quantity of agonistic behavior from the traditionally u ed isolate Con equently the present study was designed to contrast ethologically the behavior of male mice grouped individually-housed and cohabiting with females

## MATERIALS AND METHODS

### Animals

All mice used in this study were obtained from an outbred colony of the Tuck TO strain reared in the animal house facilities of University Coll ge Swansea under highly controlled conditions (described elsewhere [Brain and Bowd n 1977]) They were housed in standard opaque mouse cages measurin 30 X 1' X 11 cm with wire tops containing an ad libitum supply of food and water The mice were approximately 12 weeks old at the time of testing and there were ten animals in each of the three categories employed in this experiment namely A) Individually housed mice maintained in this condition for three weeks B) males reared cohabitating with females remaining with these animals for three weeks prior to testing and C) grouped animals maintained in groups of six s n e weaning at 18–21 days of age

### Aggression Tests

The animals were tested under white light in the dark portion of their light/dark cycle (white lights normally on at 10 PM/AM) The standard enclosure used consisted of a single rectangular Makrolon mouse cage 30 X 12 X 11 cm

The bottom was covered with fresh sawdust and a perspex plate constituted the roof so that the mice could be clearly observed via a camera positioned above. The perspex lid could be lifted to introduce the experimental mouse into the enclosure already containing the standard opponent. The standard opponent was an adult male group housed animal rendered anosmic by nasal bulb perfusion with zinc sulfate solution. Anosmic standard opponents rarely fight and have been used successfully in a number of studies [Denenberg et al 1973, Bowden and Brain 1978]. The ten mice from each category were tested for exactly ten minutes. The ten minute period was recorded on a black/white videotape machine which incorporated an electronic timer; this device enabled one to return accurately to an event where this was required; frames could be examined 20 msec apart.

### Videotape Analysis

Subsequently the tapes were analysed using an event recorder which allowed the number and total duration of particular behavioral events to be ascertained. The analysis of tapes involved categorizing the behavior of the mouse into three major categories. The categories and major sub-divisions were based on those used by Mackintosh [Mackintosh and Grant 1966, Dixon and Mackintosh 1976] (Table I). The only change that was made from the scheme was that reproductive behavior (which was evident at a very low level) was included in the category entitled social investigation rather than analysed as a separate item. All the behavior recorded referred to that of the test animal rather than the standard opponent. The behaviors of the latter animals could have been assessed separately but appeared uniform enough to ignore variabilities. The standard opponents showed fairly high incidences of flight, social and non social investigation but only very rarely anything that could be assessed as aggressive behavior.

TABLE I

| Category | Elements |
|---|---|
| Non-social investigation and flight | Explore cage, leave, wash, *self-groom*, dig, scratching, push-dig, kick-dig, scan, evade, flag, retreat, flee, freeze, defense to side, defense to back |
| Social investigation | Attend, approach, investigate, nose to nose, groom, sniff, follow, mount, push under, crawl over, push past, stretch attend |
| Aggression | Threat, attack, bite, aggressive groom, chase, offensive upright, offensive sideways |

## RESULTS

The median values and ranges for each of the observed categories are presente in Table II All the comparisons with the exception of the proportion of mice showing attack behavior which employed Fisher s exact probability test used the two tailed Mann Whitney U' test [Siegel 1956]

The most obvious finding was that males cohabitating with females showed much more overt aggression than those from the other housing conditions Alt the isolates did evidence more fighting than the group housed animals this difference was not significant The mated animals also spent less time socially investigating their opponents than the other two categories but they showed significantly more nonsocial investigation than isolates

## DISCUSSION

The finding that on all measures of aggression the mice cohabiting with female proved the most aggressive groups seems important as A) This occurred after only a relatively short period of housing B) it was evident in all animals tested and C) it occurred in a neutral arena All these features suggest that these "aggressive mice are likely to prove of great utility to workers using the mouse aggression model

These results are similar to studies that have used rats Barnett et al [1968] reported that cohabitation with females increased the aggression of wild male rats (Rattus norvegicus) displayed against unfamiliar males Flannelly and Lore [1977] found that cohabitation with intact females increased inter-male aggression a phenomenon that did not occur when males lived with ovariectomized females This latter study used laboratory rats and conflicts from a study by Barnett and Stoddart [1969] who did not find female enhancement of male aggression in laboratory bred rats

It may also be noted that the mated male mice in the present experiment spent less time socially investigating than the other two categories this is likely to be simply a consequence of their spending more time attacking the opponent afte encountering it The actual number of social encounters was not significantly lower It seems possible that males cohabiting with females are showing behavior typical of dominants (ie high aggression and low emotionality ie they spend a long time exploring) One could also suggest that the high incidence of social investigation in the individually housed category is a consequence of the prior social deprivation If this is the case the results would be reminiscent of the Latané et al [1972] experiments on rats However social investigation was f quently followed by attack or threat in individually housed mice suggesting that social investigation in this species is merely a preliminary phase of the agonis response Mated males may be more aggressive than isolates because reproductive

**…BLE II. An Ethological Comparison of Behaviors in a Ten Minute Standard Opponent Male Mice From Three Different Housing Conditions (Medians With Ranges)**

| …e | Number of mice fighting | Non-social investigation Events | Time (sec) | Social investigation Events | Time (sec) | Aggression Events | Time (sec) | Latency to first attack (sec) |
|---|---|---|---|---|---|---|---|---|
| [illegible] | 3/10 | 25 (17–33) | 346 (188–569) | 21 (17–36) | 233[c] (31–353) | 0 (0–7) | 0 (0–59) | [c]600 (345–600) |
| …em …dual …sing | 5/10 | 29 (16–54) | 347[c] (198–527) | 28 (16–39) | 344[d] (75–402) | 0 (0–17) | 2 (0–77) | 594 (52–600) |
| …from [illegible] | 10[a]/10 | 26 (16–40) | 421 (342–515) | 16 (4–39) | 78 (10–198) | 14[b] (6–19) | 81[b] (35–133) | 46[b] (0–276) |

…ers from A & B $p < 0.01$ Fisher s exact probability test
…ers from A & B $p < 0.002$ Mann Whitney U test
…ers from C $p < 0.05$ Mann Whitney U test
…ers from C $p < 0.002$ Mann Whitney U test

… stimulates gonadal function [Brain 1977] Generation of androgens is typically correlated with enhanced fighting behavior It should be noted that aggressive and sexual behavior are not necessarily related Lagerspetz and Hauto… [1967] found that in mice the opportunity to display aggressive behavior was associated subsequently with decreased sexual behavior

In summary mated males seem to have advantages compared with isolates because A) they have higher levels of fighting and B) they give a more consistent performance than traditionally employed individually housed mice

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# Interspecific Aggression and Reactivity in Rats Effects of Selective Raphe Lesions and Additional Olfactory Bulb Ablation

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Large depletion of brain 5 HT has been shown to induce mouse killing behavior in the rat. Selective lesions of the raphe nuclei have been investigated in order to determine whether the various components of the 5 HT system exert some specific control over this aggressive behavior Electrolytic lesions of the dorsal or the median raphe nucleus do not induce mouse killing whereas combined lesions of these nuclei elicit this behavior in about 407 of naive rats Consequently it appears that serotonergic neurons originating in the dorsal and median raphe nuclei work synergistically in mediating inhibitory control over mouse killing behavior Locomotor activity is increased in novel environments by each of the selective lesions and to a larger extent by combined raphe lesions 24 hours activity in resting conditions is unchanged during the light period, and increased during the dark period of the daily cycle by the various lesions As it has been shown previously that hyperactivity in response to novelty following raphe lesions is not directly related to the 5 HT decrease in the brain it appears that interspecific aggression and motor responsiveness must not be dependent on the same neural substrate within the raphe nuclei. The raphe lesions do not facilitate the elicitation of mouse killing by further olfactory bulb ablations in contrast to earlier results where bulbectomy facilitated the induction of this behavior by raphe lesions

Key words rat interspecific aggression reactivity raphe olfactory bulbs serotonin

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## INTRODUCTION

Previous research has shown that experimentally induced reductions in brain serotonin (5 HT) elicit mouse killing behavior in the rat This aggressive behavior may be induced by electrolytic lesions of the dorsal and median raphe nuclei [Grant et al, 1973 Vergnes Mack and Kempf 1973] by 5 7-dihydroxytryptamine (5 7 DHT) treatment which has specific cytotoxic effects on serotonergic neurons [Breese and Cooper 1975 Hole Johnson and Berge 1977 Paxinos and Atrens 1977 Penot et al 1978 Vergnes et al 1977] or through the inhibition of tryptophan hydroxylase by parachlorophenylalanine (PCPA) [Miczek et al 1975]

All these manipulations induce large decreases in brain 5 HT content varying from approximately 60 to 90% of control values The development of aggressive responses seems to be related to the time course of 5-HT reduction in the forebrain In contrast the hyperactivity and the hyperreactivity to external or painful stimuli do not appear regularly in these experiments and cannot be ascribed systematically to the 5 HT depletion

The terminal 5 HT projections in the forebrain originate primarily in the dorsal raphe nucleus (DRN) the median raphe nucleus (MRN) and in a more lateral and diffuse area ($B_9$ according to Fuxe and Jonsson [1974]) The axons of the DRN and the MRN converge in a medial ascending 5 HT pathway Hippocampal terminals originate mainly in the MRN and striatal terminals come mostly from the DRN [Bobillier et al 1975 Lorens and Guldberg 1974] However the 5 HT terminals in most of the forebrain structures come from cells in both the dorsal and median raphe nuclei the contribution of DRN fibers usually being twice as great as that of MRN fibers [Lorens and Guldberg 1974] The question arises whether the 5 HT mechanisms exert primarily a general and diffuse control over behavior or if some neurons control particular behaviors (eg mouse killing) through their activity in specific terminal areas To answer this question partially raphe lesions were restricted to the DRN or the MRN and their behavioral effects were compared to combined raphe lesions and to controls

It was reported previously that olfactory bulb lesions facilitate significantly the induction of mouse killing behavior by later raphe lesions [Vergnes et al 1974] or by PCPA injections [Di Chiara Camba and Spano 1971] In order to check for a possible differential facilitation resulting from previous DRN and/or MRN lesions a second experiment was performed in which the olfactory bulbs were removed in those raphe lesioned rats in which mouse killing had not been induced

## METHODS

The experiments were performed on male Wistar rats (300–500 gm) 6–8 months old housed in individual cages for one month and fed ad libitum The

animals had no experience with mice prior to the beginning of the experiments The rats were anesthetized with Nembutal® (40 mg/kg IP) and the electrolytic raph. lesions were carried out by passing a 2 mA cathodal current for 20 seconds through an electrode which had been lowered into the DRN (RAD N = 21) or the MRN (RAM N = 16) or both raphe nuclei (RADM N = 23) The following stereotaxic coordinates were used with the lambda as the reference AP = 0 3 mm (behind the lambda) ML = O DV = 6 5 mm and 7 8 mm respectively for the two nuclei Operated control animals (RAS N = 20) were treated in the same manner as the lesioned rats except that no electrode was lowered into the brain The olfactory bulbs were removed by aspiration through a midline trephine hole

At the end of the experiment the brains of all rats were fixed in 10% formalin and embedded in paraffin Sections 20 μm thick were stained with cresyl violet and the extent of the raphe and olfactory bulb lesions were assessed by microscopic examination

### General Procedure

Six days after the raphe lesion a mouse was introduced into every cage for a 4-hour period If a kill occurred another mouse was given to the rat to confirm the killing behavior On the next day the general reactivity was appraised by no in on a scale of 0 to 3 the reaction of the animal to a puff of air a gloved hand near the rat a stick thrust in front of the head and a tail pinch A mean coefficient was calculated for every group On postoperative day 7 the animals were also observed for a 6 minute period in a circular open field (75 cm in diameter and divided into 12 parts) illuminated by a 100 watt bulb 80 cm above Locomotor activity (number of parts traversed) rearing and defecation were noted for each minute

Some time between the 8th and 14th day 24 hour activity measures starting at 10 AM were made by means of an actographe The actographe consisted of a 100 cm X 20 cm X 40 cm plexiglass chamber with four infrared light beams 25 cm apart The interruptions of the light beams by the rat were recorded through four photo cells and summed every 15 minutes On postoperative days 14 21 30 and 40 mice were again placed in the rats cages for a 24 hour period and the kills noted

Six weeks after the raphe lesions the olfactory bulbs were removed in the non killing rats of each group ie N = 14 RAS N = 16 RAD N = 11 RAM N = 11 RADM animals Mouse tests were made on day 7 after the bulbectomy and then once every week Reactivity and open field behavior were again tested on day 7 Finally five weeks after the bulbectomies those rats in which mouse killing had not been induced were treated with PCPA (300 mg/kg IP) The rats were tested with a mouse two and three days later All the rats were killed after an additional observation period of ten days and the brains were removed for the histologic procedures already described

**Statistical Analysis**

Frequency data of muricide behavior were analyzed by the $\chi^2$ test. The quantitative data of the different groups were compared by nonparametric tests: Kruskal Wallis test for the overall analysis, Mann Whitney and Wilcoxon tests for the comparison of two nonpaired or two paired series of data, respectively [Siegel, 1956].

## RESULTS

As is shown in Table I, after the raphe lesions mouse killing was observed in 2/20 RAS, 2/21 RAD, 3/16 RAM, and 9/23 RADM rats. Thus only the combined dorsal and median raphe lesion was effective in inducing mouse killing. Once the aggressive behavior had been initiated, the animals killed reliably after the first kill.

Similarly, on the reactivity tests only the RADM group exhibited stronger reactions to the different stimulations than the controls ($p < 0.01$ compared to the controls, Fig 1).

The four groups differed significantly in their total locomotor activity during the six minutes in the open field ($p < 0.001$), as well as in their first minute of activity ($p < 0.05$). Individual comparisons of the six minute activity scores showed that locomotion in each of the lesioned groups was significantly greater than in the RAS group ($p < 0.001$); the RAD and RAM animals did not significantly differ from each other and were both less active than RADM animals ($p < 0.001$ and $p < 0.05$). During the first minute, only the RADM group was significantly more active than the RAS group ($p < 0.01$). In control animals (RAS group) the locomotor activity in the open field decreased 80% from the

**TABLE I** Mouse Killing Behavior Induced Successively by Various Raphe Lesions or Sham Lesion, Olfactory Bulb Ablation, and PCPA Injection (300 mg/kg)

| | Raphe lesions | | Bulbectomy | | PCPA | |
|---|---|---|---|---|---|---|
| Group[a] | n | % Killers | n | % Killers | n | % Killers |
| RAS | 20 | 10 | 14 | 50 | 7 | 86 |
| RAD | 21 | 10 | 16 | 31 | 11 | 87 |
| RAM | 16 | 19 | 11 | 45 | 6 | 100 |
| RADM | 23 | 39[b] | 11 | 45 | 6 | 83 |

[a]RAS) sham lesioned, RAD) dorsal nucleus lesioned, RAM) median nucleus-lesioned, RADM) dorsal plus median raphe nuclei lesioned rats.
[b]Significantly different from controls (RAS), $p < 0.05$.

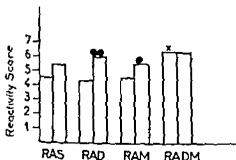



*Fig 1* Mean scores of reactivity to various stimuli in controls (RAS) dorsal raphe-lesioned (RAD) median raphe lesioned (RAM) and combined dorsal plus median raphe lesioned rats (RADM) as well as after an additional olfactory bulb ablation (stippled) X) p < 0 01 compared to controls ) p < 0 0? intragroup comparison after bulbectomy ••) p < 0 001 intragroup comparison after bulbectomy

first to the sixth minute whereas in the RAD animals there was a 39% decline and in the RAM animals there was only a 6% reduction in activity in the RADM animals locomotion increased by 11% during the 6 minute test (Fig 2) Rearings are least frequent in RADM animals but as they interfere with locomotor activity they cannot be usefully considered With respect to the defecation scores RADM animals defecated less than the three other groups (p < 0 05) which did not differ significantly

Several observations can be made on the results of the 24 hour activity measures in the actographe (Fig 3) First the activity levels of the four groups differs significantly (p < 0 001) in the first hour RAS rats being the least active (p < 0 01 compared to any other) and locomotion in the RADM animals being significantly greater than in RAD and RAM rats (p < 0 01) The RAD and RAM rats do not differ from each other However after a constant decline lasting from two to four hours the diurnal activity stabilizes at approximately the same level for each of the four groups With respect to the habituation rate the decrease of activity during the first hour divided into 15 minute intervals in the actographe (Fig 4) as well as from the first to the second hour is greater in all lesioned groups than in control animals Nevertheless the percentage decline in activity is similar in all groups In other words the time required to attain the baseline level is mainly a function of the initial activity level A comparison of the diurnal activity scores (for the four consecutive hours from 2 to 6 PM) did not reveal any significant group effect Yet during the dark period while the locomotion increases in all groups it does so to a different extent in the different groups (p < 0 001 from 2 to 6 AM between the four groups) the individual differences being similar to those observed during the first hour

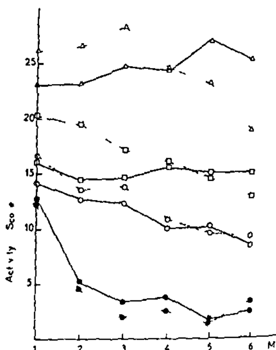



Fig 2 Locomotor activity in the open field after raphe lesions (——) and raphe-lesic followed by bulbectomy ( ) RAS controls (•) RAD dorsal raphe lesioned RAM median raphe lesioned (□) RADM dorsal plus median raphe lesioned rats (Δ)

**Bulbectomy and PCPA Results**

The olfactory bulb ablation performed in the nonkilling rats of the previo groups elicited stable killing behavior in 7/14 RAS 5/16 RAD 5/11 RAM a 5/11 RADM rats the differences are not significant Finally PCPA treatmen the nonkillers of the latter experiment induced killing in 6/7 RAS 9/11 RAD 6/6 RAM and 5/6 RADM rats without producing any sign of toxicity or any activity change Thus almost all rats were converted into killers at the end of experiments (Table 1)

The reactivity to various stimuli was increased by the olfactory bulb lesion the RAD ($p < 0\ 001$) and RAM ($p < 0\ 02$) group RAS increase was not s cant and RADMs did not increase their reactivity score which was already be after the combined dorsal plus median raphe lesion No intergroup differe was found after the olfactory bulb lesion The open field behavior was almost unchanged by the latter lesion (Fig 2) except for a slight improvement in the habituation rate in all of the raphe lesioned groups

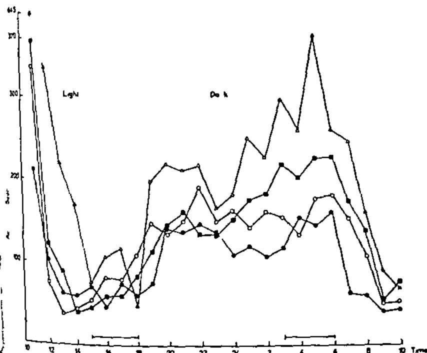



Fig 3 Twenty four hour activity in the actographe starting at 10 o clock in the morning RAS controls (•) RAD dorsal raphe lesioned (o) RAM median raphe lesioned ( ) RADM dorsal plus median raphe lesioned rats (Δ)

## Histologic Analysis

All dorsal raphe lesions destroyed at least half of the DRN and in 14 cases all or nearly all of the DRN In addition the trochlear nuclei the medial longitudinal fasciculi and the surrounding gray were partially damaged Similarly median raphe lesions destroyed at least half of the nucleus and in eight animals the totality of the MRN the tegmental nuclei of Gudden nucleus linearis and decussation of brachium conjunctivum were incidentally involved The combined raphe lesions ablated at least a part of both raphe nuclei involving as well the structures lying between these nuclei 9 rats had a total lesion of both raphe nuclei (Fig 5) No correlation was found within each group between behavioral effects and the extent of the lesions to the raphe nuclei and surrounding structures

The olfactory bulbs were always completely ablated the anterior olfactory nucleus being spared or lesioned at the anterior tip only Extension of the lesion to the anterior frontal pole was observed in only five rats

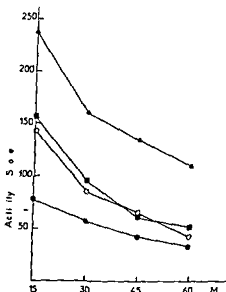



Fig 4 Locomotor activity during the first hour in the actographe in 15-minute intervals (symbols defined as in Fig 3)

## DISCUSSION

Reactivity to various external stimuli and locomotor response to a novel environment such as the open field were most increased in the dorsal plus median raphe lesioned group DRN lesions always increased locomotor reactions significantly but to a smaller extent than MRN lesions This result is in general agreement with previous reports which described an increase in open field locomotion following MRN lesions and a greater increase in locomotor activity after combined DRN MRN lesions however DRN lesions produced no change or only a non significant increase of locomotion in these experiments (Jacobs and Cohen 1976 Srebro and Lorens 1975)

In control animals locomotion elicited by introduction into the open field decreases regularly from the first to the sixth minute of the test indicating habituation to the environment In the DRN lesioned rats there was not as sharp a decrease in locomotor activity and in RAM and RADM animals there was no decrease in locomotor activity Thus habituation during a short time interval (six minutes) and in open field conditions appears to be reduced by raphe lesions In the actographe initial locomotor activity is also considerably increased by raphe lesions relations between the groups being similar to those observed in the open field However the rate of decrement of locomotor activity after the initial 15 minute period was similar in all groups until the baseline was attained

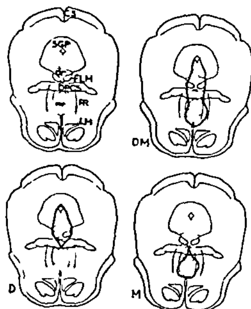



Fig 5 Outlines of typical lesions of the dorsal raphe nucleus (D) the median raphe nucleus (M) and the combined lesion of both raphe nuclei (DM) dr dorsal raphe nucleus mr median raphe nucleus CS colliculus superior DPCS decussatio pedunculorum cerebellarium superiorum *FLM* fasciculus longitudinalis medialis FR formatio reticularis LM lemniscus medialis SGP substantia grisea periventricularis (according to König JFR Klippel RA Stereotaxic Atlas of the Rat Brain)

indicating that after the initial hyperactivity in response to novelty the habituation process in resting conditions is unaffected by raphe lesions

Previous research has found however that hyperactivity following raphe lesions cannot be related simply to the fall in brain 5 HT level as PCPA or 5 7 DHT treatments do not increase locomotion in the open field or in the activ [illegible] raphe [Galey and Le Moal 1977 Hole Johnson and Berge 1977 [illegible] et al 197[illegible] Penot et al 1978 Vergnes et al 1977] Therefore [illegible] fibers passing through the raphe region may be involved in this initial hyp[illegible]activity to novelty

The daily cycle of activity is maintained in all groups The activity during the light period is low in all animals but increase of activity during the dark period larger for the raphe lesioned animals especially in the [illegible] and [illegible] groups This result is in agreement with the findings of [illegible] et al [illegible] but in slight opposition with those of [illegible] and [illegible] [19[illegible]] who found no altera[illegible]on in home cage activity following raphe lesions except [illegible] changes in lighting conditions In summary [illegible]

of general activity is unaffected by raphe lesions in resting conditions hyperactivity is elicited by increased reactivity to environmental factors (eg placement in an open field or actographe change in illumination) The magnitude of this effect is greatest after combined lesions which suggests some synergy between the two raphe nuclei

Selective lesion of the DRN or the MRN does not elicit mouse killing behavior in naive rats in contrast the combined lesion of these raphe nuclei induces killing in about 40% of the lesioned animals these results being consistent with those of earlier reports on pretested rats [Vergnes et al 1974] or nonpretested rats [Yamamoto and Ueki 1977] *The failure of either DRN or MRN lesions* themselves to elicit mouse killing suggests that the induction of this behavior after large dorsal plus median raphe lesions is not due solely to the unique projection of either nucleus Instead the extent of 5 HT depletion appears more important for the elicitation of interspecific aggression It has been shown previously that only large decreases in brain 5 HT induce killing in both naive rats and experienced nonkiller rats [Barr Gibbons and Bridges 1976] After combined raphe lesions the fall in forebrain 5 HT levels is about 70% [Grant et al 1973 Vergnes Mack and Kempf 1973] whereas it does not exceed 50% following DRN or MRN lesions [Lorens and Guldberg 1974] Similarly mousekilling is induced only if a large 5 HT depletion (about 60% to 90%) has been provoked by intraventricular 5 7 DHT injections [Breese and Cooper, 1975 Penot et al 1978] administration of 5 7 DHT into the raphe nuclei [Paxinos and Atrens 1977 Vergnes et al 1977] or into ascending serotonergic pathways [Hole Johnson and Berg 1977] or following PCPA treatment [Miczek et al 1975] 1975]

Consequently it appears that serotonergic neurons originating in the DRN and MRN work syngergistically with respect to mediating inhibitory control over mouse killing responses As the hyperactivity in response to environmental changes in raphe lesioned rats does not appear directly related to 5 HT decrease the two behavioral correlates of raphe lesions (eg mouse killing and hyperactivity) despite some apparent correlation are unlikely to be controlled by the same neural substrate

Finally earlier results suggested that removal of the olfactory bulbs facilitated the elicitation of mouse killing behavior by raphe lesions [Vergnes et al 1974] In contrast with that result we found that the lesion of one or both raphe nuclei did not increase the number of killers following olfactory bulbectomy yet almost all of these bulbectomized rats were converted into killers by a PCPA injection which presumably reduced the 5 HT content in the remaining 5 HT neurons whereas the same dose of PCPA does not consistently induce killing in nonbulbectomized rats which have had precious experience with mice Thus olfactory bulb lesions do not increase the elicitation of aggressive responses by raphe lesions if the chronological order of the lesions is reversed a finding that

suggests a qualitative difference between the complementary inhibitory influences exerted by the olfactory input and by the serotonergic system on the elicitation of interspecies aggression

## ACKNOWLEDGMENTS

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AGGRESSIVE BEHAVIOR
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# A Multivariate Analysis of Social Dominance in Children

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The social dominance behavior of dyads of unacquainted same-sex 3½-year-olds was observed in a familiar laboratory playroom under two conditions A free play situation and a situation where candy was introduced In each of the two conditions a principal components analysis was used to explore two issues the usefulness of the multivariate approach in devising a definition of dominance and the cross-situational stability of the construct In the free play session the first principal component that emerged was consistent with a theoretical definition of dominance This picture was disrupted by the introduction of candy in the second condition. However a high correlation was found between the dominance hierarchies established in each situation It was concluded that the multivariate analysis is a useful method for the study of dominance The generalizability of social dominance across settings was discussed as a possible explanation for the high cross-situational stability

Key words social dominance children multivariate analysis

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## INTRODUCTION

Research on social dominance in young children presents a picture similar t that existing in animal research Multivariate approaches have not been extens used, and a comprehensive multifaceted definition of this construct is therefoi not available Moreover dominance has been studied most often in a single setting and the validity of the behavioral indices of dominance across settings has thus not been demonstrated [Bernstein 1970] The present study represei an initial attempt to resolve these problems by identifying a variety of possible indices of dominance, observing them in two different situations and analyzing their mutual relations and cross situational stability

The selection of behaviors indicative of dominance presents two main probl First much of the research in this area has focused on overt displays of agonist behaviors McGrew [1972] devised a dominance hierarchy defined in terms of the instances in which a child won or lost a toy after a struggle with another child Strayer and Strayer [1976] following a similar approach extended the number of overt displays of agonistic behaviors incorporated in the analysis They developed a dominance structure where physical attacks and threat gestures were identified as behavioral indices of social dominance among pre schoolers

This emphasis on overt displays of agonistic behaviors tends to obscure the fact that social animals have evolved nonovert displays of agonistic behavior as means of self assertion and self abasement that often replace fighting [Jolly 1972] Chance [1967] for example developed a theory of social dominance based on attention structure in which the chief functional difference between leader and followers was that the leader was the center of the group s attention Who is looked at may thus serve as the criterion for deciding who is to be obeyed

There have been other attempts to identify nonagonistic indices of dominan Gellert [1962] studied dyadic dominance interactions using categories such as positive and negative mandates compliance and agreement These categories illustrate the second problem encountered in selecting possible indice of dominance each category comprises a large number of behaviors which have not been empirically shown to be mutually equivalent Gellert s work illustra es both the usefulness of extending the study of dominance to nonagonistic be haviors and the desirability of using a multivariate design in studying a variety of behaviors as indices of social dominance

In the present study dominance was conceptualized in terms of the reciproca channeling of social communications from one child to another ie the behavior of each child in the pair was evaluated as it related to the ongoing behavior of the other child in the pair No behavior was measured for one child independentl of the behavior of the other child in the pair This approach was patterned af er Gage s study [1978] of dominance in rats In that study a principal component

analysis yielded a multivariate definition of dominance that was reliable and consistent with predictions based on theoretical considerations and previous research In each of two situations studied – spontaneous aggression and food competition – the dominant animal tended to address overt displays of agonistic and nonagonistic behaviors to the partner but was not receptive to behaviors addressed to it The submissive animal on the other hand tolerated behaviors directed to it but tended to make few overtures toward the partner However general activity levels were not obviously less for the subordinate animals in that they would actively explore the cage when not interacting with the dominant animal While dominance was found to be a useful and reliable concept in each of the two situations there was little cross situational stability the dominant animal in the spontaneous aggression did not necessarily remain dominant when food was introduced

The present study attempted to ascertain to what extent Gage s findings would be replicated with children It was postulated that the dominant child would actively address behaviors to the partner but would be less receptive to the partner s overtures or more precisely would not orient to verbalizations from the partner the reverse would be true for the submissive child The choice of specific behaviors indicative of dominance was based on the research discussed above [Chance 1967 Gellert 1962 Strayer and Strayer 1976] On this basis it was hypothesized that the dominant child would more often initiate verbal interaction and physical contact make commands take a toy after a struggle and engage in aggressive behavior such as hit or shove and would be less likely to orient as a response to the partner s overtures

It is admittedly difficult to prove that behaviors characteristic of one species are functionally or morphologically analogous to behaviors found in another species The present study is comparable to Gage s research on rats not because the specific behaviors selected are claimed to be equivalent but because both studies share a common guideline the assumption that it may be useful to study dominance by simultaneously observing behaviors addressed to the partner and the individual s response to communications addressed to him

## GENERAL PROCEDURE

Unacquainted dyads of preschoolers were observed in a familiar playroom in two conditions that closely resembled the settings used by Gage namely a free play situation and a situation involving the sharing of food Same sex dyads were used because previous research suggested that this provision would optimally promote interaction [Blurton Jones and Konner 1973 McGrew 1972] and because there might be differences in social dominance associated with sex of the partner Unacquainted playmates were selected in order to minimize possible effects of different lengths of acquaintance

## DOMINANCE SITUATION 1

This situation was designed to observe the spontaneous social behavior of two unacquainted preschoolers of the same sex who met in a setting familiar to both of them

### Subjects

The subjects were 40 white middle class dyads (half of each sex) ranging in age from 3 0 to 4 0 (Mean = 3 1) All children were attending preschool at the time of their participation in this study They were originally recruited for a study of preschoolers social competence [Lieberman 1977] The names of the sub jects were obtained from preschool directors and the parents were contacted through a letter which was later followed by a telephone call This procedure yielded a high degree of cooperation ninety three percent of the parents con tacted agreed to participate The dangers of self selected sample were thus minimized

### Procedure

The playroom was a carpeted room with posters on the wall a couch and curtain drawn back from the windows (which were one way mirrors) It con tained a wooden car big enough to seat two children toy telephones a toy stove and cooking utensils stuffed animals and other toys The members of each dyad were selected at random except for the provision that they must be of the same sex Each child was individually familiarized with the playroom well in advance of the play session

On the day of the play session the members of the dyad were individually brought to the same playroom by familiar research assistants They were intro duced to each other outside the playroom and were then left together in the room for a play session which lasted 15 minutes and was videotaped through the one way mirror

### Measures

The following measures of social dominance were used

**Initiation of physical contact** Number of times one child touches another

**Initiation of vocalization** A verbal utterance that is addressed at the part er and occurs 10 seconds or more after the last utterance by either party

***Command/request*** *A verbal utterance that counts as a request or attempt to* get the other child to perform an action Only direct requests were used namely those to which the prefixes I command or I request could be added Sugges tions defined as statements beginning with let s were also coded under this category Commands were coded as successful or unsuccessful depending on the partner s compliance or lack of it

*Take toy* Number of times in which the child takes a toy not offered by the child who is holding it without preceding his action by a verbal request

*Win toy* After physical struggle for a toy the child succeeds in keeping it without further attempts from the other child to take the toy from him

*Orientation versus lack of orientation to source of physical contact or verbal initiation* The percentage of time that the recipient of a verbal or physical initiation orients his head towards the partner

*Hit shove* Number of times that the subject hits or shoves the partner

Th behaviors were coded directly from the video tapes by two coders working independ ntly Intercoder agreement ranged from 89% to 100% One measure hit or shove was eliminated from the analysis because it occurred only twice in ent re sample

## Results

As a rule the children started playing with the toys and interacting with each other from the beginning of the session They called each other s attention to d fferent features of the playroom shared toys and engaged in sustained con versations

Table I shows the results of the principal components analysis for the chil dr n s behavior The first principal component accounted for 49 5% of the variance The correlations in this component indicate that the dominant child tended to take a toy from the partner without encountering resistance made both successful and unsuccessful commands and requests initiated physical contact and to a lesser extent won a toy after struggling for it Submissiveness was de not d by the child s physical orientation to the initiator of verbal interaction or physical contact

**TABLE I** Correlations Eigenvalues and Percentage of the Variance for the First and Second Components of a Principal Components (PC) Analysis of Behavior in Dominance Situation 1

| | 1st PC | 2nd PC |
|---|---|---|
| Take toy | 0 92 | 0 03 |
| Unsuccessful verbal request | 0 9[illegible] | – 0 19 |
| Initiation of physical contact | 0 84 | 0 05 |
| Successful verbal request | 0 80 | 0 07 |
| Win toy after struggle | 0 46 | – 0 77 |
| Initiation of vocalization | 0 14 | 0 86 |
| Orientation to partner | -0 4[illegible] | 0 14 |
| Eigenvalues | 3 46 | 1 39 |
| % Variance | 49 4 | 19 9 |

### Discussion

The findings show that the first principal component accounted for almost half of the total variance and that the correlations on this component were high and in the predicted direction It may be concluded that the composition of the first principal component provides a potentially useful set of behaviors indexing social dominance

The results resemble those obtained by Gage [1978] in the spontaneous aggression situation with rats In both studies the first principal component accounted for almost half of the total variance and dominance could be inferred from the channeling of interactive behavior from one partner to another Two aspects of the present findings are of particular interest First aggressive behaviors (ie hit and shove) occurred so seldom that they had to be eliminated from the analysis Second win toy an agonistic behavior had a lower correlation with the first principal component than nonagonist behaviors indeed a nonagonistic behavior take toy without encountering resistance had the highest correlation on the first principal components In the absence of direct reciprocal interactions between the children both children were observed to actively explore the room thus general activity levels did not appear to differ However an independent set of measures of the activity may prove useful in future investigations of the correlates of dominance These findings may mean that even at this early age social dominance tends to be expressed through nonagonistic means of self assertion rather than through overt displays of agonistic behaviors

## DOMINANCE SITUATION 2

This situation took place immediately upon completion of the free play session An investigator entered the playroom with a bowl of M & M candy and placed it equally distant from the subject and the playmate She requested that the children not eat the candy and left the room for five minutes It was hypothesized that the request not to eat the candy would give rise to exchanges in which one child would try to persuade the other to eat or not eat the candy As in the previous situation the interaction was videotaped through a one way mirror

### Subjects

Twenty six dyads (15 boy 11 girl dyads) participated in this part of the project They were a subset of the sample used in Dominance Situation 1 but did not differ in any other way from the rest of the sample The children were paired with the same partner in this situation as in the first situation The rest of the sample could not be used because the children had already participated in the free play session by the time the present situation was designed

### Measures

All the measures used in Dominance Situation 1 were also coded in Dominance Situation 2 Two additional measures were used in assessing behavior involving candy These measures are defined below As in Dominance Situation 1 hit and shove were eliminated from the analysis because no instance of such behavior was observed to occur

*Take candy* Number of times the child takes or eats a piece of candy

*Command/request involving candy* This measure was defined in the same way as the command/request category in Dominance Situation 1 In this instance however the request or command referred specifically to the candy and involved an attempt to persuade the partner to join in eating the candy or to dissuade the partner from eating it The outcome was coded as successful or unsuccessful depending on the compliance of the partner

### Results

The majority of the dyads (75 9%) obeyed the investigator s request not to eat the candy There was considerable interest however in talking about the candy The children admonished each other not to eat it requested permission to eat it and wondered when they would be able to eat it There was much variability in the amount of time spent talking about the candy

Table II shows the results of the principal component analysis The first component accounts for 30 5% of the variance Judging from the correlations of

**TABLE II** Correlations Eigenvalues and Percent of the Variance for the First and Second Components of a Principal Components Analysis of Behavior in Dominance Situation 2

| | 1st PC | 2nd PC |
|---|---|---|
| Unsuccessful verbal request | 0 76 | 0 51 |
| Successful verbal request | 0 73 | 0 37 |
| Initiation of physical contact | 0 67 | 0 48 |
| Successful request for candy | 0 66 | 0 19 |
| Unsuccessful request for candy | 0 5[illegible] | 0 55 |
| Win toy after struggle | 0 52 | −0 05 |
| Orientation to partner | 0 51 | 0 23 |
| Take toy | −0 05 | −0 61 |
| Initiation of vocalization | −0 49 | −0 03 |
| Take candy | 0 04 | 0 40 |
| Eigenvalues | 3 05 | 1 56 |
| % Variance | 30 5 | 15 7 |

the different behavior the dominant child made successful and unsuccessful requests involving both general matters and the very specific issue of eating the candy initiated physical contact won toys after a struggle and remained oriented to the partner The submissive child initiated vocalizations to the partner Neither Take toy nor Take candy appeared to be related to dominance in this situation

### Discussion

The findings in some ways resemble and in other ways differ from the results obtained in Dominance Situation 1 When food was introduced Take toy seemed to lose its importance as an index of dominance Interestingly it was not replaced by its apparent counterpart Take candy Perhaps this was due to the effects of the investigator s request not to eat the candy Orientation to the partner which was negatively correlated in Dominance Situation 1 was positively correlated in the present situation The findings resemble those of the first principal components analysis in that general commands/requests (whether successful or unsuccessful) and initiation of physical contact retained their high positive correlation Requests/commands involving candy also had substantial positive correlations

In the Dominance Situation 1 there was a clear cut dichotomy in which dominance involved active behaviors directed towards the partner and submissiveness was reflected in orientation towards the partner This structure was apparently disrupted by the introduction of food It is possible that it was not the candy per se but rather the way in which it was introduced that disrupted the picture of dominance versus submissiveness It would be interesting to determine whether different results would be obtained by introducing a single piece of candy which could not be shared (as in Gage s study with rats) and by not instructing the children to abstain from eating the candy With the instructions used in the present study a new structural arrangement of behaviors developed in Dominance Situation 2 as compared to Dominance Situation 1

## CORRELATION BETWEEN DOMINANCE TESTS

After it had been determined that dominance was a useful construct in the two different situations the generalizability of the construct was of interest Therefore the relationship between the dominance situations was tested

### Method

A salient variables analysis was performed to determine the relation of the dominance hierarchies between the two situations as determined by the first principal components in Dominance Tests 1 and 2 Behaviors with correlations of 0 60 or more were operationally defined as salient The Z scores for the subjects were summed across these salient variables Thus a single composite score

was obtained for each child in each dominance situation composed of the sum of Z score values (standard score transformation) of the most salient behaviors as determined by the first principal component The critical correlation was obtained once the composite score was formed for each subject in each of the dominance situations

## Results

The critical correlation between the composite scores of the subjects in the two dominance situations revealed a high positive correlation (r = 0 82)

## Discussion

The high correlation between the two dominance situations on a salient variables analysis clearly suggests that even though there was some disruption of the basic behavioral patterns when food was introduced the specific order of the children in the two dominance hierarchies remained remarkably stable as determined by the behaviors most highly correlated with the first principal component (which we have chosen as our index of dominance) Thus dominance appears to be a useful and rather stable construct in describing the reciprocal channeling of social communications from one child to another

# GENERAL DISCUSSION

The aim of this paper was to explore a methodological approach outlined in a study by Gage [1978] using rats It was postulated that this approach could be used with different species and that it would yield information about the usefulness and generalizability of the concept of dominance It was also postulated that dominance could most profitably be studied by observing behaviors addressed to a partner as well as the partner's response to these overtures Several behaviors were identified as individual indices of dominance on the basis of previous research These behaviors were then observed in two different situations one involving spontaneous social interaction and the other involving behavior elicited by the presence of food In each of the two situations a principal components analysis was used to determine whether the individual indices of dominance could be combined into a single multivariate definition of the construct It was assumed that such a definition would be obtained from the first principal component because this component accounts for the largest proportion of the variance in the original set of variables The correlations of the behaviors on the first component were thus examined to determine whether their sign and size were consistent with the theoretical predictions The relative contribution of each behavior to the multivariate definition of dominance was then inferred from their correlations on the first component

In the present study, the picture that emerged was remarkably similar to that obtained in Gage s study [1978] with rats In the first situation involving spontaneous interaction the dominant child initiated physical and verbal interaction with the partner but tended not to orient as a response to the other child overtures The submissive child on the other hand was less likely to address physical and verbal behaviors to the partner but showed receptiveness by orienting to the other child This picture however, was disrupted by the introduction of food such that the dominant child oriented more toward the partner than in the spontaneous situation This could be explained in terms of the increase in attention being paid to any activity around the candy

In the present study as contrasted to the study with rats there was a high correlation between the hierarchies defined by the first principal component in each situation This difference might be attributed to differences in the two situations where food was available for the children and for the rats

The present study confirms Gage s suggestion that multivariate analysis is a useful approach to the study of dominance This construct is too complex to be *assessed through a single variable yet the use of multiple measures* presents the problem of how to combine them in order to show how each behavior is related to the concept of dominance Using the first component in a principal components analysis yields a multifaceted definition that does justice to the complexity of the concept Moreover this method may be profitably used with different species with the proviso that species appropriate behaviors should be selected as individual indices of the construct

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AGGRESSIVE BEHAVIOR
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# Evidence That Rats Discriminate Between Familiar and Unfamiliar Putative Urinary Odorants of Adult Male Conspecifics

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Adams (1976 Lehman and Adams 1977) suggested that a resident rat makes an olfactory comparison of cage odor and other rat odor prior to attacking an unfamiliar conspecific intruder The findings of the present study are consistent with the notion that rats discriminate between familiar and unfamiliar putative urinary odorants. Adult male albino rats were tested for preferences between areas treated with familiar urine (11 hours pretest exposure) unfamiliar urine (no pretest exposure) and untreated areas. Subjects (N = 12) preferred areas treated with familiar urine over ones treated with unfamiliar urine ($p < 0.05$) Also they (N = 12 per preference-test group) preferred areas treated with either urine over untreated ones (familiar versus clean $p < 0.01$ unfamiliar versus clean $p < 0.05$)

Words urine preference chemical signals, intraspecific fighting

## INTRODUCTION

Intraspecific fighting behaviors of laboratory rats are exhibited under certain conditions and not under others For example fights ordinarily occur when an animal occupying a territory is confronted by a male conspecific to which the animal has not become habituated [Moyer 1968] Hence individually reared rodents were reported to be more aggressive during encounters with

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strange male conspecifics than were group raised counterparts [Kahn 1954 Luciano and Lore 1975]

Resident intruder agonistic encounters may be under fairly specific sensory control There is evidence that presumptive scent marks are critical for onset of attack For example Adams [1976 Lehman and Adams 1977] reported that individually housed resident rats alternated between sniffing an unfamiliar con specific intruder and sniffing a Petri dish containing resident s secretions He hypothesized that the resident spent several minutes comparing the odors" of the home cage and of the other rat prior to attacking The notion that urination and onset of attack are related also is supported by the findings that castrated rats urine marked an object less than did intact males [Price 1975] and that castrated intruders were subjected to fewer attacks by a resident than were intact males [Thor and Flannelly 1976]

There is some evidence that rats do compare familiar and strange putative urinary odorants For example sexually naive adult male hooded rats preferred a cardboard-container previously occupied by a cage mate to one previously occupied by an unfamiliar conspecific [Krames and Shaw 1973] The present study was designed to provide more evidence that rats distinguish between pre sumptive urinary odorants of conspecifics

## METHOD

### Subjects

Thirty-eight sexually naive male rats of the Charles River CD strain were used Each rat was weaned at 21 days of age, and subsequently maintained individually in wire mesh cages (18 X 25 X 20 cm) on a 12 hour diurnal cycle with food and water available ad libitum except as noted below The rats then participated in a visual discrimination experiment prior to the present investigation Beginning at 60 days of age they were gentled for ten minutes daily over a nine day period Then the rats were given water for only five minutes each day while undergoing approximately four weeks of discrimination training The subjects were 137 140 days old at the beginning of their participation in the present investigation

### Procedure

Two rats were selected randomly and designated as urine donors The donors were habituated to a food deprivation schedule during the first two weeks of the experiment pellets were placed in the donors cages for one hour then removed for 11 hours and so on Urine was collected on filter paper (Whatman number 1) placed under these rats cages for the 11 hour food deprivation periods which overlapped both the light and dark phases of the diurnal cycle Urine-soaked papers were gathered at the end of each 11 hour collection period and fecal boluses were shaken off Since urine-collection papers were positioned under

cages when no food was present there was no contamination of urine by food Urine on collection papers was visualized using ultraviolet light [Desjardins Maruniak and Bronson 1973 Brown 1975] Samples of urine soaked paper (area = 25 cm²) were cut from each collection sheet

The urine samples were used as stimuli in open field preference tests Familiar urine was that to which subjects were exposed for 11 hours immediately before testing Exposure was accomplished by placing strips of urine soaked paper (area 25 cm²) in cylinders made of number 8 hardware cloth (thereby preventing subjects from contacting the paper strips) and positioning them on home-cage floors U familiar urine was that to which subjects were not exposed Clean strips of filter paper (ie not treated with urine) were also used as stimuli Samples from each donor served as familiar urine for half of the subjects in each preference test group (described below) and as unfamiliar urine for the other half of the subjects in each group

The test apparatus was a circular open field (diameter = 89 cm) The floor was covered with a clean sheet of white kraft paper divided in half by a pencil line Four fresh samples of urine soaked stimulus paper were placed equidistantly around the perimeter of one half of the apparatus four fresh samples of paper treated with the other kind of urine or clean papers (as appropriate) were positioned similarly on the other half A 6 X 6 cm square of plate glass with a 7.5-cm diameter hole drilled in its center was used to cover each paper to control for the area of exposed stimulus material These glass covers were fixed to the open field floor with double faced tape

Twelve different subjects were assigned randomly to each of three test groups The groups differed with respect to the pairs of stimulus papers placed in the open field They were familiar unfamiliar familiar-clean and unfamiliar-clean The rats were given a five minute adaptation session without stimulus papers in the apparatus on each of four days Then each rat was given one five minute preference test with the appropriate stimulus papers in the open field Preference ratios (number of rats preferring one type of stimulus sample/number of rats preferring the other) and the amounts of time spent on each half of the apparatus (time spent straddling the midline was not counted) were recorded Side of the open field on which a given sampl was placed was counterbalanced across subjects Testing was conducted under red illumination (one 25 watt incandescent bulb 1 8 m above the apparatus) approximately four hours after onset of the light phase The open field and glass plates were cleaned with 70% alcohol after each test

## RESULTS AND DISCUSSION

Preference ratios were analyzed using sign tests differences between mean time scores were evaluated with Wil oxon T tests The results are shown in Table 1

**TABLE I** Preference Ratios* and Mean Time Scores for the Three Preference Test Groups

| Stimulus samples compared | Preference ratio | Sign test P[a] | Mean time (min) ± standard error | Wilcoxon T | P[a] |
|---|---|---|---|---|---|
| Familiar vs unfamiliar | 10/2 | <0.05 | 3.11 ± 0.26 vs 1.70 ± 0.25 | 9 | <0.02 |
| Familiar vs clean | 12/0 | <0.01 | 3.12 ± 0.13 vs 1.62 ± 0.13 | 0 | <0.01 |
| Unfamiliar vs clean | 10/2 | <0.05 | 2.78 ± 0.23 vs 1.92 ± 0.23 | 15 | <0.07 |

*Number of subjects preferring first stimulus/number preferring second stimulus
[a] Two tailed

Subjects preferred the side with familiar urine over the one with unfamiliar urine Also they preferred the side with familiar urine over the clean side and the side with unfamiliar urine over the clean side

The present investigation demonstrated that adult male albino rats discriminate between familiar and unfamiliar urines the subjects preferred the former over the latter (if an organism exhibits a preference it also exhibits a discrimination and vice versa [Irwin 1958]) The findings are noteworthy inasmuch as subjects were familiarized with a given urine sample for only an 11 hour period before testing The results are not explained easily in terms of habituation or novelty If the rats had habituated or adapted to familiar urine then one would expect them to prefer the relatively novel unfamiliar urine the opposite of the present results However one experiment demonstrated that rats preferred familiar over novel (unfamiliar) stimulus objects when tested in a strange environment In contrast rats preferred novel (unfamiliar) over familiar stimulus objects when tested in a familiar environment [Sheldon 1969] Subjects in the present investigation were tested in an environment to which they had been exposed for five minutes on each of four days prior to preference testing It is difficult to say whether the rats actually did perceive the open field as a familiar environment Since Sheldon used environment familiarity as an independent variable and we did not the results of her study and ours might not be readily comparable

The data are consistent with Adams [1976 Lehman and Adams 1977] hypothesis that a resident rat distinguishes a familiar odorant (eg its own) from an unfamiliar one (eg that of a conspecific intruder) In addition the present study provided support for the notion that rats distinguish between urines from individual male conspecifics Other evidence that male rats distinguish the secretions and excretions of a familiar male conspecific from those of an unfamiliar one was derived from a cardboard-container preference test study [Krames and Shaw

973] In that experiment sexually naive male hooded rats spent more time ith their heads in the opening of a container previously occupied by a cage mate an in one previously occupied by a strange male conspecific Data which are onsistent with Adams notion were obtained in a multiple paired-comparison en field preference test experiment [Brown 1977] In that study male Lon, ans rats showed no preference when one side of the apparatus was treated with le cage mate urine and the other was treated with unfamiliar male urine The endent variable time spent actively sniffing urine treated objects in the n field was different from the one Krames and Shaw used and the one we used The present study showed that rats preferred areas treated with either urine miliar or unfamiliar) over clean areas Several other open field studies demon ted that male rats were attracted to conspecific urine For example Lon, ns subjects preferred to investigate an object treated with male conspecific ale conspecific or their own urine over an untreated one [Brown 1975 1977] n field studies also provided evidence for an attractive property of albino rat e Adult male albino rats preferred an area or object treated with conspecific e over an untreated one [Eaton 1977 Richards and Stevens 1974 Stevens Koster 1972] The question of whether rats relative preference for one type ine (eg familiar) over another (eg unfamiliar) and absolute preferences for [Carr 1974] actually are mediated by odorants must await isolation identi ion and synthesis of urinary chemical cue(s) [Beauchamp Doty Moulton Mugford 1976] to be answered

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AGGRESSIVE BEHAVIOR
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# Sex, Strain, and Housing Variables Influencing the Effects of Prior Shock Exposure on Shock-Induced Aggression

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A series of experiments was conducted to investigate sex housing conditions, and strain as possible factors influencing the interference effect of prior exposure to shock on shock-induced aggression In albino subjects, female rats and rats housed in community cages evidenced the greatest suppression in aggression following prior exposure to shock. In addition ten sessions of prior exposure to shock produced a greater suppression in shock induced fighting than 20 sessions of prior exposure to shock The prior shock effect was not obtained with hooded subjects. Responsivity to shock was also investigated to determine whether the prior exposure to shock attenuation of shock induced fighting was a consequence of reduced activity in response to shock. Responsivity to shock measured with an isometric platform accounted for less than 4% of the variance in shock induced fighting in the single experiment that obtained a correlation between responsivity and shock induced aggression.

Key words: rats, sex strain housing condition, prior shock exposure

Within recent years considerable research and theoretical discussion has been devoted to the influence of prior exposure to inescapable or uncontrollable shock on aversively controlled behavior [eg Glazer and Weiss 1976a 1976b Maier and Seligman 1976 Maier et al 1969 Seligman et al 1971] Seligman [1975] has argued that such prior exposure to uncontrollable stimulus events produces a behavioral state of helplessness that renders the subject unable to

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respond adaptively One source of data used to bolster this position has been those studies that investigated the influence of prior exposure to uncontrollable shock on subsequent aggression and reported that exposure to prior inescapable shock resulted in reduced frequencies of shock induced fighting [eg Anderson et al 1970 Maier et al 1972 Payne et al 1970 Powell and Creer 1969 Powell et al 1972 Tondat 1974] However in addition to the studies that have shown reduced shock induced aggression following exposure to inescapable shock some research has indicated that prior exposure to shock either has no influence on shock induced fighting [Knutson and Hynan 1972] or results in increased aggression [Powell et al 1972 Roberts and Larson 1967] In order to relate the Seligman [1975] model to models of aggressive behavior it is important to reconcile the differences among experiments Methodological differences among studies would seem to be a reasonable candidate to account for differences in results however several studies that obtained disparate results are quite similar procedurally Thus subject variables such as sex home cage housing conditions and strain emerge as possible variables contributing to the different effects of prior exposure to shock on shock induced fighting

## EXPERIMENT 1

The purpose of this experiment was to investigate the effects of prior shock on shock induced fighting within the context of a study that included sex of the subjects the housing conditions during the experiment and the amount of exposure to shock as additional factors In addition Glazer and Weiss [1976a 1976b] suggested that the interference effects of exposure to uncontrollable shock were associated with reduced activity in shock motivated situations To assess the viability of this alternative to the helplessness model this experiment was also designed to assess the responsivity of the subjects to shock stimuli in a nonaggression situation

### Method

**Subjects** One hundred sixty experimentally naive 90- to 95-day-old male Sprague Dawley rats and 160 experimentally naive 90 to 97-day-old female Sprague Dawley rats from the colony of the Department of Psychology at The University of Iowa were used All rats had been whelped and raised in a colony under a 12 hour light 12 hour dark cycle (lights on from 6 00 AM to 6 00 PM) and were maintained in like sex group cages from weaning until the beginning of the experiment At the start of the experiment half of the male subjects and half of the female subjects were housed six per cage in 24 X 56 X 17 8-cm stainless steel and wire mesh cages The remaining subjects were housed individually in 17 8 X 24 X 17 8-cm stainless steel and wire mesh cages All subjects had free access to food and water for the duration of the experiment and all experimental manipulations were conducted between 2 00 and 4 00 PM

Apparatus Two identical chambers were used for prior shock exposure and shock induced aggression testing Each 23 X 28 X 29-cm chamber was constructed of 6 35 mm Plexiglas with a grid floor consisting of stainless steel rods 0.3 cm in diameter spaced 1 3 cm center to center The chambers had vertical slots milled at the cente of the long walls so that a removable Plexiglas partition could be used to divide the chambers in half When divided the chambers were used for submitting subjects to prior exposure to shock and when the partition was removed the chambers were used for shock induced aggression testing Grid shock scrambled by means of a Gerbrands model G5820 scrambler was provided by a tube type constant-current dc power supply Each chamber was housed in a sound attenuated chamber with inside dimensions of 76 X 76 X 30 cm Two double one-way windows located on adjacent sides of the sound attenuated chambers permitted unobstructed observation of the rats during all procedures Fans provided ventilation and masking noise and a 7 5 W light was used to provide continuous illumination The duration and frequency of shock were controlled by conventional timers and relay circuitry During aggression testing data were recorded on electromechanical counters activated by switch closures made by trained observers

To measure responsivity to shock an isometric startle platform similar to that described by Cunningham et al [1973] was used A 7 9 X 23 X 20 2-cm shock chamber constructed of clear Plexiglas and a grid floor consisting of stainless steel rods 0.3 cm in diameter spaced 1 3 cm center to center was attached to the startle platform by an aluminum and Plexiglas frame that held the chamber 2 5 cm above the surface of the startle platform The startle platform consisted of a 13 X 27.5 X 2 54-cm plywood board that was attached at one end to a 9.5 X 13 X 2 54 cm aluminum upright The base of the aluminum upright was attached to a 41 X 30 5 X 3 1 cm plywood panel that was weighted with two 11 kg bags of sand Directly beneath the shock chamber an Astatic phono cartridge (No 24) was attached to the startle platform A 5 5-cm brass rod weighing 0 9 gm was fitted into the stylus aperture so that it maintained a position parallel to the platform The electrical output of the cartridge was passed through a solid state peak voltage detection circuit and was monitored by means of a Hewlett Packard digital voltmeter this unit provided a digital index of subject responsivity since a greater amplitude response resulted in a greater voltage output of the cartridge Shock to the grid floor of the chamber was provided by a constant current tube type dc shock source The entire startle platform was housed in an Industrial Acoustics Corporation sound attenuated chamber with inside dimensions of 50 X 92 5 X 51 3 cm Illumination was provided by a 10 W light 20 cm above the shock chamber and an exhaust fan provided ventilation and masking noise A 27 5 X 50-cm clear double window permitted observation of the rats during responsivity testing

Procedure Because of the large number of subjects all procedures were completed in a series of replications with all experimental groups represented in

each replication Following two days of adaptation to the new housing conditio all subjects were weighed and paired according to weight in like sexed pairs Within the community housing condition members of a fighting pair were not housed in the same cage Male and female pairs from both the individual housin and community housing conditions were then nonsystematically assigned to eit a prior shock (PS) condition or an adapted control (AC) condition These eight groups were further divided by assigning ten pairs each to either a 10 or 20-session condition On the first day of the experiment subjects in the 20 session PS condition were placed in the shock chambers separated by the clear Plexiglas partition Each pair was submitted to 100 shocks of 0 5 second duration at an intensity of 2 mA and an intershock interval of three seconds (onset to onset) With a 24-hour intersession interval the subjects in the PS 20 session group re ceived 20 such sessions The AC 20 session pairs were placed in the fighting chambers and separated by the partition for 20 daily five minute sessions but there was no shock delivery

During the first ten days of the experiment subjects from both the AC and PS ten session groups were removed from the home cages and handled 10–20 seconds and returned to the home cages On the 11th day of the experiment both the PC and AC groups were submitted to ten daily sessions appropriate to their group assignment On the day after the final pretest session aggression testing was initiated During ten daily sessions rat pairs were placed in the shock chambers with the partition removed and submitted to 100 shocks of 0 5 second duration at an intensity of 2 mA and an intershock interval of three seconds onset to onset Trained observers recorded instances of shock induced aggression in responses to shock when rat pairs made physical contact characterized by the response topographies of biting or boxing while in an upright posture [cf Ulrich and Azrin 1962] or when one member of a pair pawed the head and upper torso of a supine partner Since the avoidance of shock by one member of a fighting pair results in marked suppression of fighting [Knutson 1971] responses that resulted in avoidance of shock were also recorded The same observer recorded aggressive behavior and avoidance during each session Assessments of reliability among observers was calculated on a shock by shock basis and for both avoidance and attack behavior there was greater than 95% agreement among observers on a trial by trial (shock by shock) basis All subjects received pretreatment and aggression testing sessions in the same experimental chamber

Twenty four hours after the last shock induced aggression test session individual rats were tested for responsivity to shock Subjects from each group were placed individually in the responsivity test chamber and given 50 shocks of 0.3-seconds duration ranging from 0 0 (open circuit) to 0 9 mA in intensity Shocks were presented every 20 seconds and were randomized with respect to intensity The grid was cleaned between subjects This procedure was based upon the

results of a pilot study* involving 40 male and 40 female experimentally naive adult rats from the same population used in this experiment Statistically significant male female differences in responsivity only emerged at lower shock levels In addition while the mean responsivity to the graded intensity shocks had a correlation of –0 28 ($P < 0\ 07$) with shock induced fighting the correlation of mean responsivity to 2 mA shocks with shock induced fighting did not approach statistical significance Furthermore this pilot study ruled out weight of the subjects as a contributor to the individual differences in responsivity scores

Results

Aggression data Although analysis of the avoidance data indicated that avoidance behavior was not systematically related to treatments to reduce error variance all aggression analyses were based upon the percentage of shocks actually received by the pairs that resulted in shock induced fighting These aggression data were analyzed using a five factor analysis of variance with repeated measures on one factor (aggression test sessions) Although statistically significant effects of sex ($F = 65\ 09$ df = 1/144 $p < 0\ 0001$) shock history ($F = 12\ 31$ df = 1/144 $p < 0\ 001$) and aggression test sessions ($F = 2\ 92$ df = 9/1 296 $p < 0\ 0025$) were identified three important statistically significant interactions restrict the interpretability of the main effects Figure 1 shows the shock induced fighting data that reflects the statistically significant interaction of the four factors of shock history housing conditions number of pretest sessions and aggression test sessions ($F = 2\ 38$ df = 9/1 296 $p < 0\ 01$) Using the Tukey HSD [Kirk 8] a series of planned comparison tests were used to evaluate the differences between PS and AC groups within housing conditions and within number of pretest session conditions at each aggression test session Within the ten session condition the pairs from community cages submitted to the PS conditions fought less than the community-caged AC group during all test sessions ($P < 0\ 01$) The individually housed PS group fought less than the individually housed AC group during Session 3 only ($P < 0\ 01$) Within the 20 pretest session condition the community caged PS group fought less than the AC group housed in community cages during Sessions 2 and 4 ($P < 0\ 05$) The individually housed PS group evidenced less aggression than the AC individually housed group during Session 8 ($P < 0\ 05$) Thus with respect to housing shock history and number of pretest sessions at each aggression test session only the ten pretest session subjects housed in community cages evidenced a sustained and reliable reduction in fighting as a consequence of the PS condition

The statistically significant sex X shock history X aggression test session interaction ($F = 3.26$ df = 9/1 296 $P < 0\ 001$) is shown in Figure 2 Planned comparisons contrasting the PS groups with AC groups within sex across aggression sessions indicated that the PS female group fought less than the AC female

*A complete description of the experiments and these data may be obtained from the second author

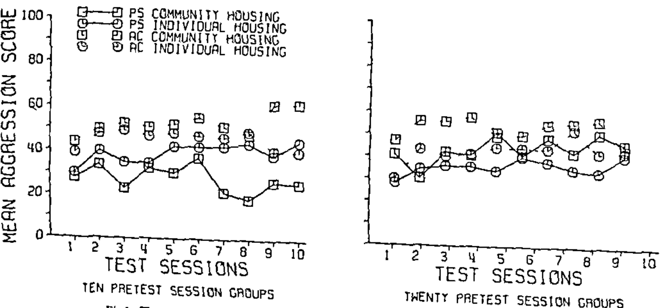



Fig 1 The mean percentage of shocks inducing aggression in all eight experimental groups of Experiment 1 at each test session.

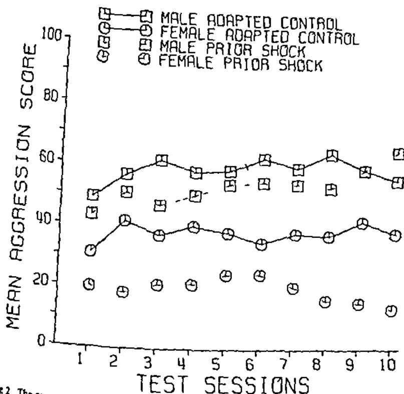



Fig 2 The mean percentage of shocks inducing aggression at each session in the four sex/shock history groups of Experiment 1 regardless of housing condition and number of pre-test sessions

group during all but Session 6 ($P < 0.01$) With respect to male subjects the PS group fought less than the AC group during Sessions 3 and 8 ($P < 0.05$) only Sex of the subject also interacted with the housing condition ($F = 10.40$ df = 1/144 $P < 0.002$) This statistically significant interaction reflects the fact that although females generally fought less than males the male female difference was was enchanced by individual housing conditions

Responsivity data Because of an electronics failure in the peak-detector circuit the responsivity scores of 20 rats were discarded These rats were distributed randomly among groups so the analysis was based upon the remaining subjects using an unweighted means procedure The responsivity to shock assessment was conducted to determine whether the PS influences on fighting could be mediated by altered reactivity to the shock stimuli To assess that possibility two separate statistical analyses were conducted The first analysis was a five-factor mixed analysis of variance with repeated measures on one factor (shock

intensity) This analysis was conducted to determine whether the influence of shock history number of preaggression test sessions sex and housing conditions would influence responsivity to the shock stimuli in a manner that paralleled the influence of those variables on shock induced aggression Although housing sex number of pretest sessions and shock level all influenced responsivity and statistically significant interactions among those variables were obtained most of those results did not relate to the effects of PS on responsivity and shock induced fighting The only responsivity difference among groups that paralleled the fighting data was the statistically significant housing X sex X shock level interaction ($F = 13.86$ $df = 8/1408$ $P < 0.0001$) Figure 3 shows the responsivity scores for each of the four housing/sex groups at each shock level and it is obvious that the male female difference was markedly increased by the individual housing condition The individually housed males displayed an increasing responsivity as a function of shock level relative to female individually housed subjects Although the community housed males were more reactive than community housed females the difference was not nearly as great as in individually housed subjects

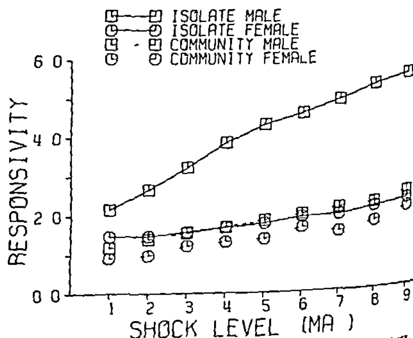



Fig 3 The mean responsivity score to the graded shock stimuli by the four housing sex condition groups of Experiment I regardless of prior shock condition The responsivity score is the peak voltage output of the Astatic cartridge mounted on the isometric startle platform

The second analysis involving responsivity measures correlated the mean re
...sivity score for both members of a pair with the mean shock induced fighting
re using the Pearson product moment correlation coefficient Based upon the
...es of 140 pairs of rats the correlation of responsivity to shock with shock
...uced fighting was 0 199 ($P < 0\ 025$) Thus individual differences among pairs
...sponsivity to shock accounted for less than 4% of the variance in shock
...uced fighting

## ...ERIMENT 2

...ecause the previous work investigating PS on shock induced aggression in this
...ra ory used hooded rats that were housed individually (Knutson and Hynan
...2) it is impossible to determine whether the PS effect on shock induced
...ession does not obtain with hooded rats or whether the individual housing in
...earlier study eliminated the possibility of detecting a PS effect The purpose
...his experiment was to investigate the effects of PS on shock induced fighting
...ooded rats using conditions identified in Experiment 1 as optimal for detect
...such differences

### ...hod

...ubjects Forty experimentally naive 95 to 102-day-old male hooded rats and 40
... rentally naive 98 to 102 day old female hooded rats from the colony of the
...artment of Psychology at The University of Iowa were used Subjects were
...lped in a colony room maintained on a light-dark schedule (lights on from
...) AM to 7 00 PM) with all experiments conducted between 1 00 and 5 00
At the start of the experiment subjects were weighed and paired according
...eight and housed six to eight per cage in 24 X 56 X 17 8-cm stainless steel
...wire mesh cages All subjects had free access to food and water for the dura
...of the experiment and members of a fighting pair were not housed in the same

...pparatus The two shock induced aggression test chambers and the responsiv
...est apparatus of Experiment 1 were used in this study
...rocedure Ten pairs of male rats and ten pairs of female rats assigned to the
...ondition were submitted to ten PS sessions following the procedure of
...eriment 1 and the ten pairs of male and ten pairs of female rats assigned to
...AC condition were placed in the chambers following the procedure of Exper
...nt 1 After ten consecutive days of exposure to the aggression test apparatus
...the PS or AC condition rat pairs were submitted to ten daily shock-induced
...aggression test sessions following the methods of Experiment 1 Twenty four
hours after the last aggression test session individual members of the pairs were
tested for responsivity to shock using the graded shock procedure of the previous
experiment

**Results**

The preliminary analysis of avoidance behavior during aggression test sessions indicated a statistically significant sex X shock history X sessions interaction ($F = 2.45$ $df = 9/324$ $P < 0.025$) This statistically significant interaction reflected nonsystematic differences among groups on three different test sessions Because of this avoidance behavior and to reduce error variance the analyzed aggression data consisted of the percentage of shocks that both members of a pair received that resulted in fighting These shock induced aggression data were analyzed by a three factor mixed analysis of variance with repeated measures on one factor (aggression test sessions) Figure 4 shows the percentage of shocks inducing fighting in each group at each aggression test session The apparent effect of the prior shock treatment was not statistically significant The statistically significant sex X sessions interaction ($F = 2.76$ $df = 9/324$ $P < 0.01$) reflects the fact that the

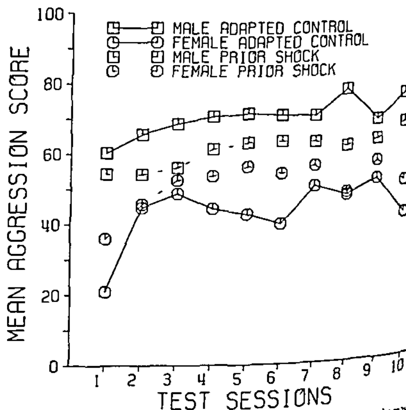



Fig 4 The mean percentage of shocks inducing aggression at each test session in the groups of hooded rats of Experiment 2

male groups fought more than the female groups during Sessions 1 2 4–6 8 and 10 ($P < 0.05$)

The responsivity data were also analyzed with a three factor mixed analysis of variance with repeated measures on one factor (shock level) This analysis indicated that the females responded more than males ($F = 16.60$ $df = 1/68$ $P < 0.001$) as well as a statistically significant main effect of shock level ($F = 44.33$ $df =$ 9/544 $P < 0.0001$) Following the procedure of Experiment 1 the relationship of mean responsivity to shock with the mean frequency of shock induced fighting was assessed using the Pearson product movement correlation coefficient That correlation ($r = -0.09$) was not statistically significant

## (PERIMENT 3

In the evaluations of responsivity to shock within the context of the investigations of prior exposure to shock and shock induced aggression the responsivity measures had to follow the assessment of shock induced fighting Otherwise the responsivity test might have influenced the fighting measures and all subjects would have been exposed to shock prior to aggression testing However it is possible that the lack of a systematic relationship between the prior shock procedures and responsivity as well as the lack of a correlation between responsivity and fighting in Experiments 1 and 2 was due to the fact that responsivity testing followed ten days of shock induced aggression testing This experiment was conducted to assess the effect of shock induced aggression testing on the responsivity measure of Experiments 1 and 2

### iod

*Subjects* Forty experimentally naive male Sprague Dawley rats from the ...ty of the Department of Psychology at The University of Iowa were used ...cts were housed in individual cages for the duration of the experiment with ... access to food and water under the light-dark cycle of Experiment 1

*Apparatus* The startle platform equipment of Experiments 1 and 2 was used to assess responsivity and one of the shock induced aggression test chambers of Experiments 1 and 2 was used

*Procedure* After two days of adaptation to the individual housing condition the rats were paired according to weight and nonsystematically assigned to two groups Individual pairs in the fighting group were placed in the fighting chamber and each pair was submitted to ten daily sessions consisting of 100 shocks of 0.5 second duration at an intensity of 2 mA presented at an intershock interval of three seconds (onset to onset) Pairs in the control condition were placed in the chamber for five minutes on ten consecutive days On the 11th day all subjects were tested for responsivity to shock using the graded shock procedure of Experiment 1 with shocks ranging from 0.0 (open circuit) to 0.9 mA

**Results and Discussion**

Responsivity data were analyzed using the mean score at each shock intensity level in a repeated measures analysis of variance A statistically significant fighting history by shock intensity interaction was obtained ($F = 2\ 63$ $df = 9/162$ $p < 0\ 01$) Post hoc comparisons between groups at each shock level indicated that the only difference between the groups was at the 0 0 mA shock level That is the groups did not differ in response to shock but the fighting group evidenced more activity on the startle platform during nonshocked trials A statistically significant influence of shock intensity ($F = 12\ 63$ $df = 9/162$ $P < 0\ 001$) paralleled directly the results of Experiment 1 These data suggest that in assessing individual differences in responsivity to shock as they relate to individual differences in shock induced fighting the responsivity measure can be made after the shock induced aggression testing

## GENERAL DISCUSSION

While demonstrating that prior exposure to uncontrollable shock can reduce shock induced aggression the results of the present experiments indicate the rather limited boundary conditions of that phenomenon However the same interactions that suggest limits for the PS effect on fighting do help clarify some of the discrepancies in the literature, especially among those studies that adopted PS and aggression inducing conditions comparable to the present experiments The Powell and Creer [1969] experiment is among those that obtained the greatest attenuation in shock induced aggression following exposure to uncontrollable shock Powell and Creer [1969] used ten sessions the number that obtained the more reliable PS effect in Experiment 1 and they housed their subjects in community cages also a contributor to the PS effect in Experiment 1 Most interesting however is the fact that Powell and Creer [1969] reported using male and female subjects without distinguishing between the sexes in their experiment Experiment 1 suggests that the PS effect demonstrated by Powell and Creer [1969] could have been potentiated by the presence of the female subjects in their groups as well as choosing the number of PS sessions and housing conditions that seem to be optimal for a PS effect on shock induced fighting

Powell and Creer [1969] included male and female subjects within groups because previous research [eg Ulrich and Azrin 1962] had indicated that sex of the subject did not influence shock induced aggression Since that time many studies [eg Conner and Levine 1969 Hutzell and Knutson 1972 Knutson and Hynan 1972 Milligan et al 1973] have indicated that sex of the subjects does contribute to obtained frequencies of shock induced fighting The present study suggests that male female differences in irritable aggression will be most ...ily

de ected in subjects housed individually during experimentation Indeed home cag housing can account for the relative differences between male and female subjects among experiments For example the difference between male female d ffe ences in the study of Knutson and Hynan [1972] and male female dif fe en es in Experiment 2 of the present study is comparable to the relative differences b tween males and females in individual cages and males and females n group cages in Experiment 1

Strain of the rat has emerged as an important factor in shock induced a_gres ion in a number of recent studies [eg Conner and Levine 1969 Milligan et al 973] and it is likely that strain differences are the best account for the dif rence between the results of Powell and Creer [1969] and Knutson and Hynan 1972] studies with respect to the influence of prior exposure to shock on shock d ced fighting Knutson and Hynan [1972] failed to show a PS effect using ale and female hooded subjects housed individually during experimentation periment 2 failed to obtain a reliable PS effect in both male and femal hooded s housed in group cages Since the PS interference effect on e cape responding also been shown to be strain dependent [Shurman and Katzev 1975 Follick te 1] the strain influence on the PS effect on aggression should not be sur sing

The influence of the biological factors of sex and strain on the PS effect on ression would seem to be very difficult to include in a helplessness [Seligman 5] account of the PS influence on evoked aggression Furthermore although conceivable that proponents of the helplessness position could argue that p housing and individual housing during experimentation could affect the ivational and cognitive aspects of helplessness the range of physiological omitants of isolation would also seem to point towards a biological media of the housing interaction with the PS effect Biological accounts of the ference effects of prior exposure to shock on avoidance-escape responding been advanced [eg Weiss et al 1976] According to Glazer and Weiss 3] a single session of brief (two seconds) and intense (4 mA) inescapable results in a transient deficit in subsequent escape avoidance responding probably mediated by a transient central neurochemical change While it ting to hypothesize that this neurochemical model could account for the the present experiments the shock parameters that result in both transient ence and the neurochemical changes [eg Weiss et al 1975] are substan if erent from the shock parameters of this study Also when obtained effect on shock induced aggression was more of a long term effect than a it effect Thus the neurochemical depletion and escape-avoidance data biological model of the interference effects of uncontrollable shock are ctly applicable to the data of this experiment or other studies that have

demonstrated that prior exposure to shock results in reduced shock induced aggression [eg Anderson et al 1970 Powell et al 1972 Payne et al 1970 Tondat, 1974]

Another alternative to the helplessness model as an account of the interferen effect of PS on aversively motivated behavior is the incompatible response hypo thesis That hypothesis suggests subjects acquire responses during prior shock th are incompatible with the response of interest in the test paradigm In a series of recent experiments Glazer and Weiss [1976a 1976] indicated that the interferen effects of PS on escape conditioning was associated with attenuated activity in shock motivated situations With respect to the PS effect on aggression con sistent with the Glazer and Weiss [1976a 1976b] data it is conceiveable that the subjects acquire shock minimizing postures that are incompatible with fightu or that they become less responsive to the shock As measured by the isometric platform the PS groups that manifested less aggression could not be considered less responsive than other groups However while significant responsivity effects would have been supportive of extending the Glazer and Weiss analysis to the shock induced aggression situation the absence of such group differences does not rule out the Glazer and Weiss hypothesis Various topography differences in response to shock that could be acquired during the PS procedure and are indis tinguishable on the isometric platform could have had an impact on fighting behavior

The data of the present experiments do not provide unequivocal support for any single theoretical account of PS influences on shock induced fighting Ther fore these data should cause researchers interested in broad questions of the effects of PS on aversively motivated behavior to pursue alternative formulatio s With respect to models of aggressive behavior the present data argue against making the broad generalization that prior exposure to uncontrollable aversive events will lower the subsequent probability of irritable aggressive behavior

## ACKNOWLEDGMENTS

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AGGRESSIVE BEHAVIOR
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# Food Deprivation Induces Conspecific Pup-Killing in Mice

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Periods of 24 to 48 hours of food deprivation reliably induced pup-killing in 30–50% of non killer male mice The behavior was prevented by previous experience with young and did not perseverate to non-deprived states Castrated males and intact females also exhibited pup-killing following food deprivation suggesting that the behavior is neither sex-dependent nor related to the presence of testosterone The findings are discussed in terms of their relationship to predatory behaviors and population dynamics.

Key words mice food deprivation pup-killing experience castration male female circulating testosterone

## INTRODUCTION

When first presented with newborn pups adult male mice typically kill and subsequently eat them Approximately 40–60% of adult male Rockland Swiss (R S) mice kill pups as compared to about 5–10% of adult females [Gandelman 1977] Animals that do not kill pups typically display maternal activities such as pup retrieval pup licking and nest building

Recent work indicates that the integrity of the olfactory system and the presence of circulating androgens are important for the display of the behavior

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Gandelman Zarrow Deneberg and Myers [1971] Gandelman [1973] and Svare Gandelman and Fortuna [unpublished observations] demonstrated that bilateral olfactory bulb removal induces pup killing behavior in non killer male and female mice of all ages and reproductive condition Castration of adult ma' s decreases the proportion of animals that exhibit pup killing and increases the number of animals that retrieve young [Gandelman and Vom Saal 1975] More over exogenous exposure to testosterone (T) reliably induces pup killing behavio in previously maternal female and neonatally gonadectomized male mice [Davis and Gandelman 1972 Gandelman and Vom Saal 1975]

In spite of the above work the functional significance of conspecific pup-killing in mice is unknown and attempts to compare and classify the behavior with other forms of aggression are non-existent Because the behavior is relatively stereotyped directed against a smaller animal and is usually followed by eating of the pup it would seem reasonable to assume that it is predatory *in natu e* On the other hand conspecific pup killing may not be a form of aggression but instead may represent eating which is controlled by the presence or absence of certain environmental conditions

A number of rat studies have shown that food deprivation increases predatory aggression toward mice and that subsequent food satiation does not attenuate the behavior [Whalen and Fehr 1964 Paul Miley and Baenninger 1971] Moreover familiarity with prey prevents hunger induced killing behavior [Paul 1972] In order to examine the possible relationship between pup killing and predatory aggression the following experiments studied whether hunger satia tion and experience with young would influence pup killing in a manner similar to that reported for predatory behaviors In addition we sought to examine whether the sex of the adult and the presence or absence of gonadal hormones would influence hunger induced pup killing In the first experiment we examined whether hunger potentiates pup killing behavior in non killer male mice and if it does is it influenced by the intensity of this motivational state

## EXPERIMENT 1

### Method

Rockland Swiss (R S) male mice 60–70 days old were isolated in 2? X 2? X 13 cm stainless-steel cages the floors of which were covered with pine shavings The animals were maintained on an ad lib feeding schedule (Purina Laboratory Chow) and kept on a 12/12 hr light/dark cycle with lights on between 7 AM and 7 PM Testing was conducted between 3–4 PM

Twenty four hours following isolation the mice were screened for pup-killing This was accomplished by placing three 1-day-old R–S pups into each animal s cage for a period of ten minutes The pups were distributed in the corners (one pup per corner) of the cage furthest from the area occupied by the male The adults behavior toward the young was classified into one of the following

ca egories 1) Retrieve – retrieved one or all pups 2) kill – killed one or all pups 3) Ignore – did not retrieve or kill pups Animals that killed or ignored pups were eliminated from the experiment

Immediately following the screening procedure forty animals had their food hoppers emptied of food Half of the animals were tested for their response toward newborn pups 24 hours later while the remaining half were tested 48 hours later A control group of 20 non-deprived animals was divided in half and tested for pup-killing either 24 or 48 hours following screening Behavioral tests we e conducted in a manner identical to that previously described with the xception that pup eating also was noted

esults

The two non-deprived control groups did not differ from each other with pect to pup killin, Therefore the data for the ten mice in each of the two ups were pooled Table I summarizes the effects of food-deprivation on non killer male mice As can be seen both 24 and 48 hours of food deprivation si,ni ficantly elevated pup killing as compared to the non-deprived control group ($\chi^2$ 10 8 df = 1 $p < 0\ 001$) However it also is evident that the intensity of hunger had no effect on pup killing since 24 hours was as effective as 48 hours of food deprivation Animals that did not kill pups usually exhibited the full repertoire of maternal behavior including pup retrieval and the assumption of nursing postures To these observers the pup killing induced by food deprivation strongly resembled spontaneous olfactory bulb and testosterone induced pup killing The avera,e latency for pup killing behavior was 85 seconds The animals

TABLE I Number of Rockland Swiss Albino Mice that Responded To 1-day-old Mouse Pups by Either Killing Ignoring or Retrieving Them

| Experiment | Group | N | Kill | Retrieve | Ignore |
|---|---|---|---|---|---|
| 1 | | | | | |
| | 24 hr deprived | 20 | 10 | 10 | 0 |
| | 48 hr deprived | 20 | 10 | 9 | 1 |
| 2 | Non-deprived | 20 | 0 | 20 | 0 |
| | Pup exposed | 15 | 3 | 10 | 3 |
| 3 | Non pup exposed | 15 | 9 | 4 | 2 |
| | Non-deprived | 15[a] | 0 | 15 | 0 |
| | Deprived | | 11 | 3 | 1 |
| | Non-deprived | | 1 | 14 | 0 |
| | Deprived | | 14 | 1 | 0 |
| 4 | Non-deprived | | 0 | 13 | 2 |
| | Castrated | 17 | 7 | 10 | 0 |
| 5 | Sham-castrated | 17 | 9 | 7 | 1 |
| | Male | 20 | 7 | 1- | 1 |
| | Female | 20 | 6 | 14 | 0 |

[a] Cyclicly deprived and sated

usually would sniff a single pup for 10 to 30 seconds prior to attacking it The animals would then repeatedly bite the pup and begin to consume it Animals that killed young usually exhibited this response toward all three pups but did not always consume all three

These results clearly show that food deprivation induces pup killing and eating In the next experiment we examined whether prior experience with pups would prevent pup killing in food deprived non killer males

## EXPERIMENT 2

### Method

Adult male mice were screened for pup killing behavior as previously described and only those animals that exhibited maternal activities were used in the experiment At 9 AM on the following day half of the group (N = 15) was presented with six 1-day old R S mouse pups At 5 PM the same day the pups were removed and replaced by six other 1-day-old pups This procedure was continued for seven days The other half of the group (N = 15) was not presented with pups during the same period At 3 PM on the ninth day the animals had their food hoppers emptied of food Tests for pup killing were conducted 24 hours later (day 10) as previously described

### Results

Casual observations indicated that the animals that were fostered pups showed maternal activities each day for the duration of the pup exposure period Table 1 shows the results of the behavioral tests It is evident that prior pup exposure prevented food deprivation induced killing Significantly fewer food-deprived animals that were chronically exposed to pups exhibited pup killing as compared to food-deprived animals that were not exposed to pups ($X^2 = 4\ 66$ df = 1 $p < 0\ 05$)

If non killing experience with pups prevents subsequent food-deprivation induced pup killing we speculated that the reverse might also be true namely pup killing during deprivation might serve to perseverate the response to conditions of satiation We examined this question by studying pup killing in animals cyclicly food deprived and sated

## EXPERIMENT 3

### Method

Adult male mice that were scored as maternal during a screening test were food deprived for 24 hours and then retested for pup killing behavior Fifteen

...mals that killed pups during the re test were used in the experiment The ...imals were allowed free access to food for a period of 48 hours beginning ...mediately following the retest The animals were then tested for their pup killing behavior as described earlier Following the test the animals were allowed ...4 hours of free access to food followed by a period of 24 hours of food deprivation Tests for pup killing were conducted at the end of the deprivation period This cycle of testing under conditions of food deprivation and satiation was repeated until the animals had been tested three times while sated and twice while deprived

Results

Table I shows the number of animals that killed pups under conditions of ... food deprivation and satiation As seen in the table the predominant response following food deprivation was pup killing while animals usually exhibited maternal retrieval following satiation Kruskall Wallis Tests showed that ...h change in the pup killing behavior as a function of the cyclic change in motivational state was highly significant ($Q = 44.1$ $df = 4$ $p < 0.001$) These ...ta ...dicate that killing experience during food deprivation does not serve to ...entuate the behavior during non-deprived states

The previous findings suggest that hunger induces pup killing in non killer ...les However testosterone injections are known to increase pup killing be... ...r in mice [Davis and Gandelman 1972] and some reports indicate that ...ular function increase during starvation [Grewall Mickelsen and Hufs ...71] Thus an alternate explanation is that pup killing in non killer males is ... to food-deprivation induced elevations in testosterone and not hunger per se ...method for examining this hypothesis is to test castrated animals for food ...rivation induced killing This tactic was employed in the following experiment

## ...ERIMENT 4

...od

...dult R S males were screened for pup killing behavior and only those animals ...r trieved pups were used in the experiment On the day following screening ...of the animals in each group ($N = 17$) were bilaterally castrated under ether ...hesia while the remaining half ($N = 17$) were sham-operated Seven days follow... ...urgery the animals were again screened for pup killing behavior This was done ...ler to insure that pup killing was not induced by isolation Following the ...d screening test the animals were food deprived for 24 hours and tested for ...illing (ie eighth post surgical day)

## Results

Castrated and sham-operated animals continued to show maternal activi during the second screening test prior to the imposition of food-deprivation Table I shows that similar numbers of animals in both groups killed pups fo ing food deprivation thus indicating that testosterone elevations probably responsible for food-deprivation induced killing To further eliminate this e planation we performed testosterone (T) radioimmunoassay [Bartke Steel Musto and Caldwell 1973] on the plasma of equal groups (N = 10/group) non deprived maternal animals 24 hour deprived animals that killed pups a hour deprived animals that retrieved young The blood was collected immec following the behavioral test since we have previously reported that circula T is not affected by behavioral interactions with pups [Svare Bartke and Gandelman 1977] The median plasma T levels were 4 44 ng/ml for non-de maternal animals 0 31 ng/ml for deprived killer animals and 0 27 ng/ml for deprived maternal animals While it is interesting to note that deprivation wa accompanied by dramatic reductions in circulating T the results clearly sho that an elevation in plasma T is not responsible for food deprivation induced killing

If testosterone is not important for pup killing behavior induced by food deprivation one would predict that non killer female mice would also kill y after being deprived of food for 24 hours We tested this hypothesis in the fc ing experiment

## EXPERIMENT 5

### Method

Adult male and female mice were screened for pup killing behavior as de scribed previously Twenty male and twenty female adults that retri ved new young were deprived of food for 24 hours beginning immediately following tl screening test The number of animals killing pups following the deprivation period was noted

### Results

The results are summarized in Table I As can be seen both male and fema adults killed pups following food deprivation Furthermore the sexes did not differ from each other with respect to the number of animals exhibiting the be havior These findings indicate that food-deprivation induced pup killing is no related to the presence of testosterone and non killer females like males possess the substrate for the behavior

## DISCUSSION

The results show that periods of 24 to 48 hours of food deprivation reliably induce pup-killing behavior in 30–50% of non killer male mice The results also show that food deprivation induced pup killing does not perseverate to non deprived states Similar results have been obtained in the rat by Paul and Kupferschmidt [1975] They found that 57% of adult male rats kill neonatal rat pups following long term (23 hours of food deprivation for 11 days) food deprivation and subsequent food satiation reduces the number of animals killing pups While food deprivation is known to enhance the predatory behavior of rats toward mice [Heimstra and Newton 1961 Heimstra 1965] subsequent food satiation does not attenuate the response [Paul 1972 Paul Miley and Baenninger 1971 Whalen and Fehr 1964] Thus pup killing and muricide would seem to differ with respect to the effects of food satiation on the killing response

The findings also show that continuous exposure to pups prevents subsequent food-deprivation induced pup killing in mice In contrast to our findings Paul and Kupferschmidt [1975] reported that prior experience with neonatal rat pups does not prevent subsequent hunger induced killing in the rat The difference between our findings and those of Paul and Kupferschmidt most likely is due to the chronic pup exposure used in our experiments (continuous contact with young for eight days) as opposed to the more acute exposure (daily 30 minute encounters with young for eight days) used by the latter investigators Regardless our findings are consistent with those showing the loss of spontaneous and hunger induced predatory responses in animals either reared with prey or receiving exposure to prey as adults [Kuo 1930 Galef 1970 Johnson Desisto and Koenig 1972 Paul Miley and Mazzagatti 1973]

Although androgens are important for spontaneous pup killing in mice [Gandelman 1972 1973] it is evident from several of our findings that testicular hormones do not modulate hunger induced pup killing First castration did not reduce the proportion of males exhibiting hunger induced pup killing Second male mice that killed pups following food deprivation did not have higher circulating T levels than animals that did not kill pups following food withdrawal Finally female mice were as likely as male mice to kill pups following food deprivation The literature concerning the possible endocrine involvement in predatory behavior is inconclusive Although Paul Miley and Baenninger [1971] reported that Long Evans female rats tended to kill mice more frequently than their male counterparts most studies indicate that the sexes do not differ significantly in predatory aggression [Karli 1956 Fox 1969] Inselman Temkin and Flynn [1973] have shown that the presence or absence of gonadal hormones in male and female cats modulates the latency to attack an anesthetized rat after

electrical stimulation of the hypothalamus In contrast to the above finding Bernard [1974] reported that testicular hormones do not influence frog killing in rats

To summarize our findings as well as those of others 1) Testosterone injection olfactory bulb removal and as shown here food deprivation facilitate pup-killing behavior 2) Previous chronic exposure to young prevents subsequent food-deprivation induced pup killing 3) Castrated males and intact females are as likely as intact males to exhibit pup killing following food deprivation As previously reviewed the relationship between pup killing and predatory behavior is not clear The response is obviously destructive in nature but more research on possible emotional accompaniments and relationships to eating must be completed before the response can be adequately characterized

Finally these findings may be important in understanding the growth and decline of populations The incidence of pup killing increases in mouse populations as density increases [Brown 1953] It is presumed that density-dependent changes such as endocrine alterations are responsible for these behavioral changes However our findings suggest that other factors such as the reduced availability of conventional food may be responsible for the conspecific cannibalism observed in high population densities

## ACKNOWLEDGMENTS

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AGGRESSIVE BEHAVIOR
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# Aversive Odors of Male Mice: Experiential and Castration Effects, and the Predictability of the Outcomes of Agonistic Encounters

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The relationship between the aversive urine odors of adult male mice and their agonistic interactions was examined The urine of 28 isolated intact donors was tested for its aversiveness before the donors had won or lost an agonistic encounter by spotting a portion of an open field with their urine Group-housed males (n = 28) each tested with the urine of an ultimate winner and loser as well as a castrate avoided both intact types. The urine of castrates was not aversive Another group of subjects (n 28) tested with urine collected following the encounter between donors, provided identical results A second experiment examined the aversiveness of urine from 24 isolate mice, and their responsiveness to urine of other isolates, prior to their encounter The urine was not highly aversive to the isolates. However winners and losers differed in their responsiveness, as ultimate winners exhibited greater aversion. The results are discussed with regard to territorial maintenance via odors, and how differential responsiveness to odors may influence the outcomes of agonistic encounters.

Key words aggression, mice urine aversiveness

A considerable amount of evidence has accumulated establishing the importance of olfactory cues in the regulation of rodent social interactions [Bronson 1971 Cheal 1975 Schultz and Tapp 1973] particularly agonistic interactions [Lee and Brake 1971 Ropartz 1968] For example urine odors of male mice

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have been found to be a major influencing factor in agonistic encounters between male mice [Mackintosh and Grant 1966 Mugford and Nowell 1970]

A technique frequently used to investigate the influence of urine on the agonistic behavior of male mice involves the swabbing of urine onto the coats of the castrate opponents of trained fighters [Jones and Nowell 1973a Mugford and Nowell 1970] The results indicate the incidence of attack by the fighters is a function of the urine source The urine of highly aggressive male donors significantly increased aggressive behavior relative to water swabbed controls while urine of recently defeated or submissive males had little effect [Jones and Nowell 1973a Mugford and Nowell 1970] Kessler et al [1975] found differences in the effectiveness of the urine of various inbred mouse strains to promote aggression suggesting the influence of genetic factors However a limitation of the technique of swabbing castrates with urine and using them as opponent animals is the possible confounding of the urine stimuli with the behavioral stimuli emitted by the castrate That is behavioral variation in the castrates arising from differences in the urine types applied to them may be partly responsible for the observed variation in the aggression of the fighters Essentially the problem is that the castrates may not be the truly standardized opponents they are often considered to be [eg Jones and Nowell 1973a Kessler et al 1975 Mugford and Nowell 1970]

A characteristic of male mouse urine which is closely related to its apparent aggression promoting properties is its aversiveness to other males Jones and Nowell [1973b] found that group housed males avoided a portion of an open field spotted with the urine of conspecifics spending most of the time on the clean untreated portion The effect was found to be androgen-dependent as castration eliminated the aversiveness of the donor s urine while testosterone replaced it in a dose-dependent manner [Jones and Nowell 1974a] The coagulating gland an androgen dependent gland which secretes directly into the urine was determined to be the source of the aversive urinary substance [Jones and Nowell 1973c]

Just as for the aggression promoting properties of urine the aversive effects appear to be influenced by previous agonistic experience Aggressive males were found to produce urine highly aversive to group housed subjects while those subjects responding to the urine of a defeated donor spent nearly equal time on each side of the field [Jones and Nowell 1973a 1974b] Jones and Nowell [1974b] suggested the differences were due to a lower secretion of the coagulating gland as a result of reduced androgen output in those animals that had been defeated A concomitant increase in the aversiveness of the victor s urine possibly as a result of increased androgen output [Rose et al 1974 Rose et al 197 ] was not suggested Furthermore possible differences in the urine aversiveness of victors and losers prior to their fighting may account for a portion of the dif

ferences observ d after fighting The first experiment of this study explored the poss b lity of differences in urine aversiveness before fighting as well as the nature of the change in urine aversiveness due to the experience of an a onistic encounter (e e her winning or losing a fight) This was accomplished by taking measures of the avers v ness of an animal s urine both before and after a fighting episode

There may be differences in the quality of the urine odors of victors and losers prior to their engaging in fighting (ie differences which are predictive of the out come) This would suggest individual differences in the quality of the urine odors to be a factor influencing how two strangers respond to one another and hence influencing the nature of their relationship Likewise there may be individual differences in an animal s responsiveness to particular urine odors with such dif ferences also affecting the interaction between two mice The author has observed that one of the first responses made by each animal of a pair when placed together in a neutral area is urination which is effective in spreading stimuli to which the other may respond The present proposal i that the quality of the cues each animal puts down and the quality of the behavioral responses of ea h animal to the urine odors of the other are important in determining how the encounter is resolved A second experiment was conducted to determined if the outcome of an agonistic interaction between two mice is predictable on the basis of differences in 1) the quality of their urine odors in terms of its aversiveness to another mouse and/or 2) the quality of their behavior in terms of their re sponsiveness to another s urine

## EXPERIMENT 1

As briefly discussed previously this experiment was designed to replicate and extend the findings of Jones and Nowell [1973a 1974a b] More precisely this experiment was de igned to 1) replicate the finding that prior to an agonist ic encounter the urine of intact mice is aversive while that of castrates is not [Jones and Nowell 1974a] 2) replicate the finding that following an agonistic inter action winners produce aversive urine while losers do not [Jones and Nowell 1973a 1974b] 3) determine if differences in urine aversiveness exist which are predictive of the outcome of an agonistic encounter and 4) determine what type of changes in urine aversiveness if any occur from the pre to the postfighting aversion tests (ie what effect winning or losing has on the aversiveness of an animal s urine)

### Method

The subjects and urine donors were 112 male Swiss Webster albino mice pur chased from the Ancare Corporation Manhasset New York when approxi mately 30 days old Upon delivery the animals were housed in groups of four

and maintained under a 12 hour 12-hour light dark cycle with lights on at 1 00 AM and off at 1 00 PM. Except where noted, food and water were supplied continuously to both subjects and donors.

Forty eight of the mice were arbitrarily selected to serve as urine donors and were isolated from 50 days of age to the end of the experiment. Sixteen of the urine donors were castrated on the day of isolation while the other 32 remained intact. The remaining 64 animals stayed in groups and served as responding subjects, 32 in the prefighting and 32 in the postfighting aversion tests. Only animals residing in groups in which no wounding or deaths occurred were used as urine donors or responding subjects. This was done to minimize the effects of prior dominance/subordinance relations in the establishment of winning and losing donors, and to minimize variation in aversion test scores due to dominance/subordinance variation in the responding subjects.

The apparatus employed to collect urine was a 24 X 18 X 18 cm rat metabolism cage adapted for use with mice by exchanging the feces screen for a 4 77 squares/cm mesh screen. Approximately 25 days after the beginning of isolation each donor was housed individually in a metabolism cage. The pairings for later aggression testing were determined at this time, with donors matched according to weight. However, animals previously isolated from the same group were not paired in order to eliminate the effects of any lingering familiarity. After a 48- to 72 hour period of acclimatization to the metabolism cage (ie, after approximately four weeks of isolation) urine was collected for use in the prefighting aversion tests. Urine was obtained over a 16-to 18 hour period between 4 00 PM and 10 00 AM during which food was removed to prevent contamination of the urine. The urine samples were stored in airtight glass receptacles and were used within seven hours of collection.

Urine aversion testing took place in a 45 X 45-cm open field with 45-cm-high walls. All walls were made of unpainted aluminum except for an 18-cm high strip of Plexiglas at the base of one wall to permit observation of the subject. The floor of the apparatus was a table upon which unprinted newsprint had been placed. This technique facilitated the elimination of urine odors following each trial by simply removing the soiled newsprint, wiping the table with a damp sponge, and placing a clean sheet under the open field. Ten spots of urine (each being approximately 0 125 ml) were distributed approximately equidistant throughout one half of the field. The subject was placed under a 10 X 10 X 10-cm Plexiglas box in the center of the field. Twenty seconds later the box was removed and the time spent on each side of the field was measured for a five minute period. All testing took place in a darkened room under red light illumination. During a trial the observer was approximately 1 5 m from the field concealed behind a fiberboard screen containing a viewing hole 10 cm in diameter. Testing took place one half to five hours into the dark period.

In order to minimize emotional responses to the novelty of the aversion test situation each of the group housed subjects received a ten minute session in the clean aversion test apparatus within 24 hours of the actual testing On the day of test g each subject received three trials separated by approximately one hou Each subject was tested with the urine of both members of a particular donor pair as well as one castrate donor in a counterbalanced order This re sult d in each donor s urine being tested against two different group-housed subjects The side to which the urine was applied was alternated both within and between subjects

urine was applied was alternated both within and between subj cts

The winner and loser of each donor pair was not known during the first (prefighting) aversion test This procedure ensured that the observer was operat ing b'ind when taking the measures of aversiveness of intact donor urine during the prefighting session It should also be clear that the donors did not serve as subjects but simply supplied the stimuli in the form of urine to which the sub jects responded

Aggression testing of the donor pairs began 48 hours after the initial aversion t s All aggression testing took place in a 30 X 30-cm open field with 30-cm high walls Three walls were made of unpainted aluminum with the fourth Plexiglas Again the field was placed on a table covered by unprinted newsprint A mouse was placed on each side of the arena separated from its opponent by a Plexiglas barrier One animal of each pair had been previously marked on the tail to allow identification Twenty seconds later the barrier was lifted and observation began A winner and loser from each intact pair was established during three sessions conducted once every 48 hours The initial two sessions were 30 minutes in duration while the third was run to a criterion of submission on the part of one animal of each pair the latency to which was recorded The criterion consisted of 30 successive defensive (submissive) postures often accompanied by high pitched squeaking and in the absence of tailrattling or fighting back This criterion was adopted to ensure that one animal had actually been defeated and was achieved in 90% of the encounters between intact animals during pilot observations The duration of the third session for the castrate donor pairs which exhibited little fighting behavior was determined by the mean time to criterion of the in tact donor pairs All testing took place in a darkened room under red light illumination one half to five hours into the dark period The observer was con cealed behind a fiberboard screen

Immediately following the last session of aggression testing urine was again collected from the donors using the procedure previously described The aversion test procedure following the establishment of a winner and loser in each pair was identical to the prefighting session with an independent group of 32 group housed mice serving as subjects The three urine samples to which a

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Urine aversion testing took place in a 45 X 45 cm open field with 45-cm high walls All walls were made of unpainted aluminum except for an 18-cm high strip of Plexiglas at the base of one wall to permit observation of the subject The floor of the apparatus was a table upon which unprinted newsprint had been placed This technique facilitated the elimination of urine odors following each trial by simply removing the soiled newsprint wiping the table with a damp sponge and placing a clean sheet under the open field Ten spots of urine (totaling approximately 0 125 ml) were distributed approximately equidistant throughout one half of the field The subject was placed under a 10 X 10 X 10-cm Plexiglas box in the center of the field Twenty seconds later the box was removed and the time spent on each side of the field was measured for a five minute period All testing took place in a darkened room under red light illumination During a trial the observer was approximately 1 5 m from the field concealed behind a fiberboard screen containing a viewing hole 10 cm in diameter Tests took place one half to five hours into the dark period

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Immediately following the last session of aggression testing urine was again lected from the donors using the procedure previously described The version test procedure following the establishment of a winner and loser in each pair was identical to the prefighting session with an independent group of 3? group housed mice serving as subjects The three urine samples to which a

of the defeat to which the losers were subjected While each study allowed approximately the same amount of time for interaction different strains of mice were used Strain differences in aggression may have resulted in variation in the severity of defeat between the two studies For example the loser in the present study may have suffered a much more severe defeat resulting in release of an alarm odor [Carr et al 1970] causing subjects to avoid the location of the urine Alternatively while it did not appear to be so to the observer the defeat of the losers may not have been severe enough to have resulted in a reduction in urine aversiveness Fortunately a measure suggested to be indicative of the severity of defeat namely the time required to reach the criterion of submission during the session was obtained It is argued that the more submissive or more severely defeated donor would reach the criterion sooner than a less submissive one During the third session some losers were found to submit to nearly every approach by the winning animal and hence would reach the criterion very quickly Other losers would submit only when attacked and occasionally fought back extending the session Also variation in the attack frequency of the winners would have an effect on the time to criterion For example a pair including a very aggressive winner who defeated his opponent by continuously attacking him would have a short third session The correlation between the time to submission for each loser and the measure of his urine aversiveness (mean of the two subjects responding to the urine during the postfighting session) provides evidence concerning the two complementary explanations of the failure to replicate the results of Jones and Nowell [1973a 1974b] A Spearman rank correlation resulted in a significant positive correlation between the two measures ($R = 0\,659$ $n = 14$ $P < 0\,02$ two tailed) This suggests as a tentative explanation subject to future experimental test that the losers of the present study had not been defeated severely enough to result in a reduction in their urine aversiveness However this explanation does not account for the lack of some trend towards lower aversiveness of the loser s urine

## EXPERIMENT 2

The second experiment examined pre-encounter differences between winners and losers on the following two variables 1) their urine aversiveness as determined by other animals response to it and 2) their responsiveness (aversion) to the urine of conspecifics Although no pre-encounter differences in urine aversiveness predictive of the winner were found in Experiment 1 the measure was taken in the present experiment There were two reasons for doing so First as is indicated in the methods below the design of the experiment allowed simultaneously obtaining a measure of urine aversiveness when assessing responsiveness to other s urine Secondly Experiments 1 and 2 differed in terms of the nature of the responding animals In Experiment 1 the responders were group-housed males,

while Experiment 2 employed isolates It is argued that the use of isolates allows a more valid determination of the influence of the urine aversiveness factor on the outcome of the encounter That is if the desire is to determine the influence of urine aversiveness on the encounter between two isolate animals the appropriate animal with which to measure the variable would be an isolate

Method

Thirty two male mice obtained as in Experiment 1 served as both donors and subjects At 50 days of age each animal was isolated for approximately four weeks prior to the beginning of the experiment

Urine collection proceeded as in Experiment 1 with 48 to 72 hour acclimatization to the metabolism cage The pairings for aggression testing also followed the procedure of Experiment 1 In the aversion tests each member of a particular pair was tested with the urine of each member of another pair This resulted in all 32 animals being tested with the urine of two other animals as well as each subject s own urine being tested against two other subjects In other words for each subject a measure of both its responsiveness to other s urine and the other s responsiveness to its urine was obtained It should be noted that in this experiment donors also served as subjects as opposed to Experiment 1 in which the data came from independent groups of group-housed animals Aversion testing was conducted in the same manner as in Experiment 1

Forty-eight hours after aversion testing aggression tests began Each pair was observed for three sessions as in Experiment 1 with the same criterion of submission for termination of Session 3

The design of the present study permitted categorization of the aversion test data into four cells based upon the status of the responding animal (winner or loser) and the status of the donor That is each subject found to be a winner during aggression testing had previously responded to the urine of two donor animals one of which was later found to be a winner (designated the WW cell) and the other found to be a loser (WL) Likewise each losing subject had responded to the urine from a donor destined to win (LW) and another destined to lose (LL) It should be emphasized that neither the status of the responding subject nor the status of the donor animals was known prior to aggression testing producing the favorable circumstance of collecting the aversion data under blind conditions

Results and Discussion

As in Experiment 1 14 of the 16 pairs of animals (87 5%) reached an outcome as defined by the criterion of submission However to place the data for each pair into the appropriate cell (ie WW WL, LW or LL) required that the pair to which they responded reach an outcome and vice versa Thus the total number of pairs and hence data points per cell was reduced to 12

The mean time spent on the clean side of the open field as a function of responder status and donor status is provided in Table II A Wilcoxon matched sample signed ranks test on the donor factor collapsed across levels of responder indicated no difference between winners and losers ($z = 1\ 12$ $n = 24$ $P > 0.20$ two tailed) That is just as Experiment 1 demonstrated animals could not be differentiated as winners and losers based upon pre-encounter differences in urine aversiveness A comparison between levels of the responder factor collapsed across the donor factor indicated a significant difference between winners and losers before their agonistic encounter ($z = 2\ 39$ $n = 24$ $P < 0\ 02$ two tailed) Those animals destined to win exhibited a slight aversion to the urine while the ultimate losers showed a slight attraction when summed across the donor factor

Examination of the values in Table II indicates large differences in the responses of isolate animals compared to the group housed animals in Experiment 1 (see Table I) While the urine of isolate intact donors was aversive to the group-housed animals isolate responders showed little deviation from the random response level of 150 seconds (overall mean = 149 68 seconds) In terms of the four cells defined by the two levels of each factor only one (LW) appears to deviate greatly from 150 seconds (sign test $n = 12$ $P < 0\ 05$ two tailed) and this is towards greater attractiveness rather than greater aversiveness In analysis of variance terms the deviation of the single cell is suggestive of an interaction between the responder and donor factors That is while a difference was found between the responsiveness of winners and losers the strength of the difference appeared to be a function of the level of the donor factor Comparisons indicated such an effect in that winners and losers differed in their responsiveness to urine of animals destined to win (ie WW vs LW $z = 2\ 39$ $n = 12$ $P < 0\ 02$ two-tailed) but not to urine of animals destined to lose (ie WL vs LL, $z = 0.59$ $n = 12$

TABLE II Mean Time (in seconds ± standard error) Spent on Clean Side of Open Field by Isolate Male Mice in Experiment 2[a]

| | Donor status | | | |
|---|---|---|---|---|
| | Winner | | Loser | |
| Responder status | Time | Aversion ratio[b] | Time | Aversion ratio |
| Winner | 159 02 ± 4 81 | 8/12 ns | 155 10 ± 5 76 | 8/12 ns |
| Loser | 131 08 ± 7 48 | 2/12* | 153 52 ± 4 62 | 8/1? ns |

[a]P values refer to comparisons with random response value of 150 seconds and were determined by sign tests
[b]Defined as the number of subjects scoring greater than 150 seconds divided by the number o subjects
*$P < 0\ 05$ (two tailed) ns nonsignificant

$P > 0.20$ two tailed) Thus the pre encounter differences between winners and losers were primarily due to large differences when responding to the urine of animals destined to win More specifically the difference was due to the attractiveness of such urine to those animals which later lost an encounter These results are quite similar to previous results [Sawyer unpublished study] using a ld sto k of mice and their soiled bedding as the stimulus odor While there was overall reduction in the response measures (ie greater attractiveness) across els relative to the present experiment the differences between particular 's were very similar with the greatest attraction exhibited when animals that er lost responded to the soiled bedding of males destined to win

The present experiment suggests that differential responsiveness to urine odors y influence the outcome of the encounter between two mice It should be ognized that the behavioral effect of urine stimuli presented alone may not be same as when stimuli are presented in conjunction with a live animal How these data suggest the hypothesis that in an isolate pair of inexperien ed the animal exhibiting the greatest attraction to the other will generally be ated If this is the case the fact that the first attack of an encounter was rally credited to the ultimate winner (20 of 28 in both experiments 08 $P < 0.05$ two-tailed) suggests that the attracted animal was possibly vulnerable or in some way may have provoked the attack To answer these ions fully it will be necessary to go beyond simply classifying animals as ers and losers or as first attackers Rather it will require careful analysis of iteraction between the two animals in terms of particular behaviors such as aching avoiding nosing etc and their relationship or correlation with the me of the agonistic encounter [Cairns and Scholz 1973]

## RAL DISCUSSION

use urine and its aversive properties to other males have been hypothesized e a territorial function in nature Jones and Nowell [1973a] suggested could deter conspecifics from entering an area they inhabit by marking it rine Furthermore based upon their previous results only aggressive ant males would produce urine aversive enough to aid in the maintenance rea While the results of laboratory studies such as the present one may readily generalizable to the natural situation the present experiments do m to support the proposal of Jones and Nowell [1973a] First the initial ment found the urine of winning and losing mice to be equally aversive suggested that the failure of the loser s urine to decrease in aversiveness was the lack of a severe enough defeat However under natural conditions a means of escape is available defeats would probably be even less severe

Secondly the urine was not found to elicit extreme aversion as subjects in Experiment I were found to spend a minimum of 40% of the time on the treated side of the open field The difference between this figure and the corresponding 30% reported by Jones and Nowell [1973a] may be due to differences in the amount of urine used or the size of the field However with regards to natural conditions the present study used what was probably a large amount of urine considering the size of the treated area Furthermore urine odors were not found to be at all aversive to isolates While isolation is not comparable to the natural existence of mice the same can be said for group housing [Crowcroft 1966] However it is also true that only a slight aversion to the urine odors may be required to prevent conspecifics from entering an area That is just as in aggression testing during aversion testing no means of escape was available as would be the case in nature Had escape been possible the responding animal may have done so Future research is necessary to answer this question Thus while it does appear that urine odors can indicate the present or previous occupation of an area by another animal and possibly serve a general dispersal function it is not clear that such odors are effective in maintaining the integrity of a territory

As was previously noted comparison of Experiments 1 and 2 indicated large differences between group housed and isolate mice in terms of their responsiveness to the urine of isolate donors While the comparison is between two different experiments and should be interpreted with caution it is suggested that the differences may be reflective of physiological differences between grouped and isolate mice [eg Welch and Welch 1969] and may well be reflected in the frequently noted group isolate difference in agonistic behavior [eg Valzelli 1969 Hyde and Sawyer Note 1]

The suggestion from Experiment 2 that the attraction of one animal of a pair to the other makes it more vulnerable and/or provokes attack from the latter is reminiscent of Scott and Fredericson s [1951] conclusion that pain and threat are important factors in the initiation of fighting behaviors among inexperienced mice That is an animal attracted to the odors emitted by another could be perceived as threatening by the latter Furthermore actual investigation such as genital nosing could become painful inducing an attack Coupled with the finding that being the first attacker confers some advantage to that animal this can explain the basis for the influence of differential responsiveness to urine odors on the outcome of an agonistic encounter Further research is necessary to specify the precise nature of any such influence

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AGGRESSIVE BEHAVIOR
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# Some Aspects of Predatory Behavior

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Predatory behavior is conceived of as a loose chain of responses including searching for relevant stimuli hunting or chasing potential prey capturing or attacking prey and killing and feeding on prey These aspects, which may occur independently are described and discussed separately with an emphasis on mammalian species of carnivores Particular attention is paid to opportunism in prey selection, specific searching images with their possible antecedents the role of hunger in prey attack and the phenomenon of surplus killing Finally a discussion of mouse killing by rats attempts to show similarities between this and other more traditional examples of predation

Key words predation predatory behavior

## INTRODUCTION

Animals are not always struggling for existence They spend most of their time doing nothing in particular But when they do begin they spend the greater part of their lives eating — *Charles Elton*

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Predation is typically thought of as the killing and eating of one animal by another as such it is a natural form of exploitation of nature s resources This paper is about the ambiguities surrounding this definition and similar ones and emphasizes predatory behavior in mammals particularly carnivores To many people predation seems unfair brutal and even evil its only saving grace being that killing of prey always results in nourishment of the predator This sequence is by no means inevitable however and the relationships of predation to feeding and aggressive behavior will be examined Vertebrate predators appear generally to be opportunists willing to eat that which is available and not necessarily goaded to kill by hunger or the necessity of feeding An examination of a laboratory model of predation in the form of mouse killing by rats concludes the paper

A great deal of research has been done on predation by ecologists Because of their focus on population questions however relatively little is known about the behavior of individual predators [for example see Ewer 1973] Actual instan of predation by mammals are extraordinarily difficult to observe while they are happening and antecedent and consequent events are usually even more diffi ult to document Ecologists interested in predation typically must rely on analysis of predator and prey census data and/or carcass and predator droppings data [Hornocker 1970] In recent years a sizable literature on optimal foraging strategies has developed [Krebs 1973] but the prey in these experiments are almost exclusively plants or insects and to describe the events as prey capture i usually dramatic exaggeration Compared to the large literature in psychology initiation and termination of feeding responses in the laboratory there is ably little experiment and theory on the other aspects of food getting Animals outside the laboratory do not receive dietetically-correct pellets or mash in foo hoppers before feeding they must search for or select their food and then c capture and subdue it in the case of carnivores all the while on guard against predators attempting to do the same to them Certainly predation would ap to be a rich field for investigation by those interested in animal behavior and its motivation

## PREDATION AS A RESPONSE CHAIN

In an exceptionally thorough series of laboratory experiments Beukema [1968] investigated the roles of hunger and experience in the predatory behav of three spined sticklebacks by measuring aspects of what he termed prey "ra including the probabilities of encountering discovering (fixating) gra ping a eating or rejecting the prey provided Beukema found that the probabilities of grasping and eating prey increased with hours of food deprivation as did prey capture responses the number of swimming bursts and the distance predators swam The probability of prey discovery did not vary with hunger whereas

ion of staying still varied inversely with hunger Gardner [1964] conceptualized prey catching in jumping spiders as a chain of responses each of which lead normally to the stimuli for the subsequent response Orientation toward prey pursuit crouching and exposing the mouth attachment to a strand to limit the fall and jumping at the prey She found that once pursuit began the probability of completing the response chain was high and that hunger (or drive level) no longer mattered although hunger did effect the probability of initial responses

Following such analyses we may think of predation as involving some or all of the following component activities 1) Searching for relevant stimuli 2) hunting or chasing potential prey 3) capturing and/or attacking prey 4) killing the prey and 5) feeding on the prey Normally predatory behavior will involve all these activities in the order presented here but the sequence may terminate at any point for a variety of reasons For example Estes and Goddard [1967] found that African hunting dogs (Lycaon pictus) killed 85% of the prey they chased but occasionally simply gave up chases which sometimes lasted more than 25 minutes Mech [1966] found that out of 120 moose detected there were only six successful kills by a pack of 16 wolves Hornocker [1970] reported that lynx captured 18/43 snowshoe hares (42%) while lions fail more than they succeed and tigers capture prey in one out of 20 or 30 attempts according to Schaller [1972] Habitat differences may account for differences in the frequency with which prey are ignored or rejected — ie in which the predatory sequence breaks off after searching or hunting and capturing For example Reichert [1973] found that Agelenopsis aperta a desert-dwelling spider rejected only 1% of captured prey on its sheet web whereas another spider species Linyphia triangularis (Clerck) rejected 21% [Turnbull 1960] of the much more abundant prey in its deciduous woodland habitat Searching and chasing may be unnecessary if a predator simply finds itself among a large group of prey as in the case reported by Kruuk [1972] in which foxes decimated a large colony of black headed gulls which apparently did not attempt to flee Leyhausen [1973] asserts that lying in wait for prey stalking chasing seizing killing and eating prey each has *action specific energies* of its own and denies that there is a single unitary prey-catching drive to which all these activities are subordinate

## SEARCHING FOR RELEVANT STIMULI

This step in the postulated predatory sequence probably represents a general characteristic of predators Exploration and activity have many of the characteristics of drive states that do not require antecedent deficiencies to become manifest [Koch 1956 Harlow 1953 Kavanau 1967] Traditionally experimental psychology has treated animals as if they were passive requiring deprivation or danger to energize them into activity The idea that an animal will not do anything unless prompted by information from its buccal cavity stomach or

Predation is typically thought of as the killing and eating of one animal by another as such it is a natural form of exploitation of nature s resources This paper is about the ambiguities surrounding this definition and similar ones an emphasizes predatory behavior in mammals particularly carnivores To many people predation seems unfair brutal and even evil its only saving grace bein that killing of prey always results in nourishment of the predator This sequen is by no means inevitable however and the relationships of predation to feedi and aggressive behavior will be examined Vertebrate predators appear generall to be opportunists willing to eat that which is available and not necessarily goaded to kill by hunger or the necessity of feeding An examination of a laboratory model of predation in the form of mouse killing by rats concludes the paper

A great deal of research has been done on predation by ecologists Because of their focus on population questions however relatively little is known about th behavior of individual predators [for example see Ewer 1973] Actual instanc of predation by mammals are extraordinarily difficult to observe while they are happening and antecedent and consequent events are usually even more difficu to document Ecologists interested in predation typically must rely on analysis predator and prey census data and/or carcass and predator droppings data [Hornocker 1970] In recent years a sizable literature on *optimal foraging* strategies has developed [Krebs 1973] but the prey in these experiments are almost exclusively plants or insects and to describe the events as prey capture is usually dramatic exaggeration Compared to the large literature in psychology o initiation and termination of feeding responses in the laboratory there is remark ably little experiment and theory on the other aspects of food-getting Animals outside the laboratory do not receive dietetically-correct pellets or mash in food hoppers before feeding they must search for or select their food and then chase *capture and subdue it in the case of carnivores* all the while on guard against predators attempting to do the same to them Certainly predation would appear to be a rich field for investigation by those interested in animal behavior and its motivation

## PREDATION AS A RESPONSE CHAIN

*In an exceptionally thorough series of laboratory experiments* Beukema [1968] investigated the roles of hunger and experience in the predatory behav of three spined sticklebacks by measuring aspects of what he termed prey "nd including the probabilities of encountering discovering (fixating) grasp [illegible] eating or rejecting the prey provided Beukema found that the probabilities of grasping and eating prey increased with hours of food deprivation as d d [illegible] capture responses the number of swimming bursts and the distance predat [illegible] swam The probability of prey discovery did not vary with hun er whereas [illegible]

prey whereas table scraps and garbage birds and invertebrates constituted secondary prey Eberhard [1954] found much the same result in a study of food habits of house cats in Pennsylvania Coman and Brunner [1972] found that feral house cats in Victoria Australia preyed on house mice Mus musculus in non bush im proved a eas but did not do so in bush areas where mice were less available (but not absent) Toner [1956] reported that house cats on an Ontario farm rarely took birds although they were available they captured shrews and moles b t did not eat them even when hungry Chipmunks (Tamias striatus) Northern flying squirrels (Glaucomys) red back mice (Clethrionomys) and meadow jumping mice (Zapus hudsonicus) were taken occasionally but meadow voles (Microtus pennsylvanicus) were overwhelmingly the major prey during that period of the year when domestic cat food was made available in smaller quantities (April–December)

An opportunity to observe the development of new prey choices by baboons (Papio cynocephalus) has recently led to the fascinating data reported by Harding and Strum [1976] A baboon troop near Gilgil in Kenya which had been under observation for some time already began to exploit a previously neglected food resourc in the form of young Thompson s gazelle and Cape hare Over the course of five or six years an increasingly carnivorous feeding pattern began to emerge At first only a few individuals captured mammalian prey and did so ... one but gradually males females and even juvenile baboons began to capture and feed on young gazelles

One major question is how does an organism become an appropriate prey object ? An answer that has been suggested by Luuk Tinbergen [1960] is the concept of the specific searching image Tinbergen sampled the composition of food found in a pine wood in Holland and compared this potential food distribution with that actually brought by adult titmice (Parus spec div ) to their nestlings Also abundant prey species were at first very poorly represented in the food brought during the next week the proportion of these species brought to the young suddenly increased greatly without any obvious change in prey density or size in the hunted territory The increase appeared in different adult pairs at different times (which were unrelated to the appearance of prey in the hunted territories) On the basis of such observations Tinbergen suggested that individual predators may form images of the specific prey for which they are searching which results in a rapid disproportionate increase in the risk of being captured for the specific prey species Many naturalists have reported anecdotes supporting such a notion In addition to the perceptual aspect Tinbergen s concept also implies a motivational aspect Certain prey species may become appropriate after they have been experienced as rewarding to the predator who then actively searches for that specific species The phenomenon may be seen as the appetitive counterpart of conditioned aversions which have been so intensively studied by psychologists interested in learning phenomena during recent years [Garcia Clarke and Hankins 1973] A

conditioned aversion develops when a particular stimulus associated with feedi... (such as taste) is followed by illness the predator rapidly acquires a lasting aversion to the associated stimulus Seligman [1970] has suggested that such associations are rapidly acquired because particular species are prepared to associate taste and illness If that is true it may well be that predators are prepared to associate particular aspects of prey (appearance sound presence of fur or feathers) with beneficial consequences as well If an experience of poisoning is more disastrous (Type II error) to a predator than ignoring potenti... beneficial prey species (Type I error) it should follow that conditioned aversio... are acquired more rapidly than specific search images The question is an interesting one for further research on behavioral evolution

Unambiguous evidence for the existence of specific search images is difficult to find and plausible alternative hypotheses usually exist Mook Mook and Heikens [1960] reported sudden rapid increases in the risk due to predation of just-emerged Bupalus moths that were fed by adult titmice to the nestlings Beukema [1968] found evidence of specific search images in three spined stickl... backs preying on Tubifex worms in a complex honey comb tank Introduction ... a new prey (pieces of Enchytraeus) was followed by disporportionate increases ... the probabilities of fixating grasping and eating Enchytraeus by the stickleback... The probability of rejecting Tubifex was increased by the presence of the new prey even though the predators stomachs were far from full and even though th... new prey were not visible at the time of rejection of the accustomed prey When Drosophila were the introduced prey none of these changes were observed and independent tests suggested that consumption of Drosophila was minimal Beukema suggested the concept of prey specific hungers to account for his results since various measures of hunger increased on Enchytraeus while decreasing on Tubifex One rather fascinating finding of Beukema s also deserves note After Enchytraeus (which were white) were introduced the fixating and grasping responses to white inedible objects as a percentage of all responses to inedible objects showed a dramatic increase to nearly 100% Such generalization strongly suggests a change in searching strategy by the predators

Errington [1967] describes a threshold value for predation on bobwhite quail wintering near Prairie du Sac Wisconsin Over several winters if the population of quail remained below 330 then predation losses were low and represented the rate expected if an occasional hawk owl or fox captured a couple of birds from a covey When the population of quail exceeded 330 it could draw quit... severe predation as long as many birds existed in excess of the threshold

The essential idea behind the specific search image concept seems to be that a predator is actively looking for a particular prey Given a predator equally familiar with two equally numerous and difficult to-catch prey species if the predator has a specific search image for one of them then that prey will be taken in greater numbers Put this way the concept sounds like nothing more than

another way of describin, the existence of a preference But the perceptual aspect is also implied – namely that the predator has an image or template of that species being searched for The existence of such an image is obviously difficult to test

If it can be shown that two prey species are equally attractive to the predator as food (ie killed equally often when presented under controlled conditions in which hunting is not required) then we might need the specific search ima e to expla d fferential predation A more stringent experimental criterion mi ht be impos d That th predator fails to hunt for or rejects one prey species even if it is encountered while searching for the other I am not at all convinced that the con ept of specific searching images could stand th appl ation of these two criteria in controlled exp riments under natural or semi natural conditions

An intriguing sou ce of data might be the enormous lore on sport fishing Angle s are well known for their beliefs in the efficacy of particular lures for the spec e predators that they hunt If there is some basis in reality for these beliefs we m ht be able to determine the critical characteristics of the si n stimuli for predatory attack by fish Specific search images are in a sense temporary (rather tha instinctive) releasing mechanisms for predatory attack althou h the capacity of a species to form them may be phylogenetically determined Since search images involve changes over time in what is preyed upon it appears hi hly un likely that specific search images are instinctive or species typical except in the sense that predators are more likely to respond to certain stimulus aspects such as mov ment or that particular predators may be biologically prepared to de velop search images for particular types of prev and thus are usually found to prey on tho e species when available

## CAPTURING AND/OR ATTACKING PREY

In accounts of both vertebrate and invertebrate predation a common finding s that capturing and killing prey is don in a highly stereotyped manner that is characteristic of the particular predator but may vary according to the particular prey An intriguing invertebrate example is the spider Agelenopsis aperta in wh h individuals develop specific techniques for handling various prey types [Riechert 1974] Thus species does exhibit a general prey capture routine in volving entanglement of prev that land on the spider s sheet platform but no attempt at all is made to entangle some kinds of prey whereas others are wrapped n s lk at the rostral or caudal end only Prey with powerful rear legs for example grasshoppers are not entangled with silk at the rear [Riechert personal communication]

Among carnivorous mammals the teeth are used for seizing and killing [Ley hausen 1973] and only in the most highly developed species are the forelimbs used for grasping prey pulling it close and holding it The nape bite shown by

most Felidae is a killing bite because behavior and morphology are ideally suited for severing the spinal cord The canine teeth and the orientation of the bite are suited to each other according to Leyhausen [1973] and there is sufficient injury to the cervical spinal cord Attacks that result in death by strangulation caused by a prolonged bite from underneath or biting and holding the prey s nose have also been reported in the larger Felidae such as lions [Schaller 1972] especially when large prey such as Cape buffalo are attacked

Leyhausen [1956] describes the way in which foxes locate small prey and then perform a characteristic mouse jump in which the forepaws and nose strike the prey simultaneously Fox [1969] reported the same response in captive grey and Arctic foxes as well as in coyotes and van Lawick-Goodall and van Lawick [1970] reported seeing the response in jackals Canidae also go after larger prey Wolves normally capture their prey by chasing and bring down moose for example by leaping up and biting at rump or flanks If a moose in good condition stands and defends itself it is unlikely to be killed [Mech 1966] African hunting dogs (Lycaon pictus) also attack by leaping and biting the flank of their prey In contrast to the Felidae canids typically chase prey over distances as great as five miles for wolves [Crisler 1956] and even longer for canids on open plains such as the Serengeti Felids appear to rely on stealth surprise and bursts of speed The motivational aspects of relative persistence in the two groups have not been rigorously examined the effect of hunger for example on when cats and dogs give up attempting to capture prey could provide important data for psychological theory

## KILLING AND FEEDING ON PREY

A perusal of the literature on predation reveals a striking fact There are frequent reports of predators attacking and killing prey animals and not eating them subsequently A familiar example is the propensity of cats to attack and kill certain rodents moles and shrews [Toner 1956] without eating them even though the cats may be hungry Errington [1967] recounts many field observations of similar phenomena including seeing a family of foxes that killed 160 chickens without eating them At a time when foxes were subsisting largely on meadow mice (Microtus) Errington [1947 p 31] recounted seeing fox dens with a heap of uneaten bodies of harvest mice (Reithodontomys) outside Foxes kill weasels and moles but rarely eat them unless very hungry Instances of individual lynxes killing two or three foxes in a night have been reported Unless very hungry a lynx is unlikely to eat fox [Errington 1967 p 56] Kruuk [1972] presented a number of field observations of what he calls surplus killing and attempted to elucidate adaptive consequences of such behavior for individual predators and/or the species A population of black headed gulls nesting in a non ideal site on the English coast was decimated by several foxes About 200 gulls were killed by

each fox and only about 3% of the bodies showed signs of having been fed upon Killing was done on dark nights according to Kruuk and the prey apparently put up littl resistance signs of struggle being practically absent In contrast in the same area only one of 31 rabbit carcasses was *not* eaten Observations of caching (i nn bodies presumably for future use) parallel the killing results Gulls and terns were not cached whereas rabbits frequently were Kruuk also reported killing of Thompson s gazelle by hyenas in the Serengeti Plan of Tanzania In a large pe centage of cases only damage to central nervous system was found the rest of the carcass being untouched Again the evidence suggested little resistance by th gazelles which are among the swiftest but most abundant prey of large mammalian predators in the Serengeti In African wild dogs (Lycaon pictus) Kruuk observed some relationship between killing and eating Those individuals that did not eat available prey (which was killed by others) showed no tendency to join in the actual killing attacks He concluded that chasing and attacking were separately motivated responses Additional observations of surplus killing by other predators were also presented by Kruuk Failure to eat killed prey has been reported in leopards (killing goats) lions (killing wildebeest) polar bears (killing narwhals) and bear and wolves (killing caribou calves)

Since the assumption is common that predators attack and kill only what th y n d to feed on for survival what are we to make of such reports? Kruuk suggests a n mber of possible adaptive consequences of such behavior including making food available for later use (although caching is obviously more effective in cold b omes where carcasses decay less rapidly) making abundant food available for young of the species and gaining experience in attacking and killing Like many such hypotheses about adaptive significance these have a post hoc character are difficult to test and are rarely tested Leyhausen [1965] suggests that in the Felidae attacking and killing prey may lead to eating or may l ad to more killing in a kind of self reinforcing positive feedback system [Baenninger 1974] Kruuk [1972] concludes that eating may occur anywhere in a series of kills or may not occur at all but that an adaptive criterion for behavior suggests that predators should not search hunt catch or kill prey if they are satiated unless they are able to use the prey later In addition to requiring energy expenditure a certain amount of danger to the predator is always associated with chasing or attacking prey since su h behavior at the very least makes the predator more vulnerable and/or conspicuous to its own predators The prey may be dangerous in its own right as for example when lions that attack antelope are occasionally slashed by their prey s horns [Schaller 1972] In addition of course surplus killing is simply extravagant although it clearly provides food for a variety of scavengers and is therefore not wasteful Mueller [1973] found evidence in hawks that hunger was related to feeding and killin He deprived the birds of food for varyin time periods and showed that both the percenta e of body weight consumed in dead mice and the number of mice killed increased with deprivation interval To my

knowledge no writers have denied that such a relationship usually exists What has been argued is that not all instances of killing by predators result from hunger To say that if an animal is hungry it is more likely to kill and eat prey is not to say that instances of killing and eating are always due to hunger

The idea that predation by predators may sometimes involve their killing without feeding is contrary to our preconceptions We have despite evidence to the contrary [Johnson 1972] been taught to believe that our species is the only one that kills for the excitement of the chase or simply for the sake of killing This belief it seems to me may simply reflect our persistent human tendency to see our species as somehow special set apart from other animals by noble motives or in this case by depths of depravity which they do not share

*Schaller [1973 p 237]* states flatly *All predators kill more than they need* if they have the opportunity to do so Hunger is not always a prerequisite for hunting and killing As an example he recounts an incident on the Mukoma Pla n of the Serengeti During a night storm Thompson s gazelle massed on the plain and several hyenas raced among them blindly biting and ripping at the gazelles In the morning Schaller and Hans Kruuk examined the resulting carna e Over a hundred killed or maimed gazelles with deep bite wounds skin torn off their flanks legs dangling uselessly while the satiated hyenas lay among the bodies Such extravagance is not common but with the variety of predators and scavengers on the East African plains these killing binges are not wasteful of biomass since sharing of kills by mammals birds and invertebrates is common But the point to keep in mind is that given the opportunity predators appear motivated to kill available prey in excess of actual caloric needs Given the re markable ability of some species to monitor their caloric needs when required to work in the laboratory for food there is clearly somethin more than hunger acting to motivate such surplus killing Epstein and Teitelbaum [1960] showed for example that laboratory rats maintained a constant calori intake when diets of differing caloric content were delivered directly to their stoma ls contingent upon bar presses by the rats

I have argued elsewhere [Baenninger 1974] that aggressive attacks in many species appear to be a self reinforcing activity ie the probability that attacks will be performed may increase following successful non punishing performance of attacks The killing binges reported by Kruuk [1972] and by Schall r [1973] are precisely what one would expect if attacks were self reinforcing In the absence of any danger or punishment each attack that is performed increases the probability of subsequent attacks until fatigue or the absence of more animals to attack brings an end to the series of attacks Normally prey animals are either scarce and must be found and hunted or they flee or defend themselves with the weapons at their disposal when attacked by predators Either of these situat ons would remove the condition for an attacking binge by the predator and the rarity with which such binges have been reported may simply attest to the fa t

that prey are rarely abundant obvious and unmotivated to flee or defend themselves

Now it is certainly true that being a predator for a living is usually hard work because prey are not often unwilling to hide flee or defend themselves Among canids for example wolves [Mech 1966] and African wild dogs [Estes and Goddard 1967] may chase their quarry for several miles although Estes and Goddard found that effective packs took much less time to bring down their prey (4–6 minutes) To engage in a great deal of energy-expending work without gaining or taking advantage of additional energy is clearly wasteful from the point of view of the individual predator and does not routinely occur particularly in areas where prey is scarce Hornocker [1970] in discussing predation by mountain lions in Idaho concluded that they utilized each kill in his study area and ate about 70% of each mule deer they killed leaving rumen bones feet and hide The percentage eaten was even higher for smaller deer Hornocker estimated that 4–6 pounds of meat were needed daily by adult mountain lions that they needed one deer every 7–10 days in winter but could go longer without deer in summer when small prey were more available However deer were relatively scarce and presented some danger to their attacker so that the absence of killing binges is not surprising

The fact that population sizes of predators are typically limited by the population sizes of their potential prey is another indication that wasteful killing is unlikely to be found routinely in normal circumstances For example Kruuk [1970] concluded that hyena populations were limited by food supply in two ways In the Serengeti National Park the supply of food for cubs was the limiting factor since ungulate prey migrate over long distances whereas in the Ngorongoro Crater the limiting factor appeared to be food supply for adult hyenas since in a relatively closed area of 250 km² little migration is possible

When one observes the teeming abundance and variety of animals in protected regions near the equator as for example in the National Parks of Kenya and Tanzania or on Barro Colorado Island in the Canal Zone it is hard to think of a predator s life as a difficult one It is probably true in such regions that predators are more selective about what they eat than in more northerly or temperate regions such as those studied by North American ecologists mammalian predators are more likely to behave opportunistically when opportunities are few

Data from field studies that bear on the issue of whether particular predators favor particular prey species are often difficult to interpret unambiguously Rudnai [1974] for example reported that male kongoni (Coke s hartebeest) are killed by lions disproportionately to their numbers in Nairobi Park Males are about 37% of the population yet nearly 80% of the kongoni killed by lions in the park were male according to Rudnai s tally of lion predation from 1968 to 1972 Either lions prefer males or male kongoni are more at risk Perhaps they are more readily found alone or vulnerable At some times young zebra make up 89% of

once were the order clearly includes species that behave in a carnivorous piscivorous and/or insectivorous manner Rattus norvegicus is certainly not a member of the order Carnivora and yet since 1956 when Pierre Karli first studied killing by rats in the laboratory it has been clear that rats may behave like carnivores by attacking and killing mice Whether attacks and killing of mice by rats are predatory or aggressive is an issue [Van Hemel 1975 O Boyle 1974] Moyer has suggested that one kind of aggression may be predatory aggression" which he defines as attacks made on the characteristic prey of a species th is not very helpful since only about 20–30% of laboratory rats kill mice a figure that can hardly qualify mice as characteristic prey of laboratory rats That such rats differ from wild rats is however suggested by Karli s finding [1956] that approximately 70% of wild rats kill in the laboratory

In any natural situation euryphagous species show two different adjustments to changes in prey density [Holling 1961] First a functional response occurs which involves changes in feeding behavior as a function of prey availability As prey density increases an increase in the rate of capture of that prey by the predator species should be shown Examples of such behavior have been documented by Holling for several rodent species feeding on insect larvae and by Riechert [1974] for spiders feeding on a variety of insects

A plausible explanation of the difference between wild and laboratory rats in their propensity to attack and kill mice may stem from this functional response Mice as prey have not typically been available to laboratory rats but wild rats are likely to encounter mice toward which they may behave in a predatory fashion A vague domestication hypothesis is usually put forth to account for the difference in percentage of rats attacking mice the notion being that laboratory rats have somehow become degenerate over the generations that they have been kept free of the ecological pressures that shaped the species behavior and thus are no longer predators A possible test to distinguish between the domestication hypothesis and a functional response hypothesis would be to make mice available to rats periodically as prey in the lab over several successive generations The breeding percentage of mouse killers should gradually increase if the functional response hypothesis is correct although the rats would still be domesticated

A second adjustment of a predator species to increases in prey density is to increase its reproductive rate and/or its numbers this is known as the numerical response and it obviously requires more time than a functional response Increased prey numbers may lead at first to increased prey consumption by the predator followed by increased likelihood of predator survival faster development greater fecundity and possibly improved offspring viability This pattern has been documented for a number of animal groups by Andrewartha and Birch [1954] and is not of particular concern here

Neural mechanisms for attacking and killing mice appear to be present in most rats so that the question of why some rats kill should perhaps be turned around

Why do 70–80% of laboratory rats fail to kill? Karli found that removal of a sub... ...ual amount of frontal lobe tissue changed about half of a sample of laboratory ...nkiller rats into killers Vogel and Leaf [1972] found that administration of ...ocarpine to laboratory rats eventually induced all of them to kill mice although the rats were not as reliable killers as those that attacked mice spontaneously Hoebel and his colleagues [eg King and Hoebel 1968] have shown that administration of certain cholinergic drugs will also induce nonkilling rats to kill mice as will electrical stimulation of sites in the lateral hypothalamus These sites are ...ide ...cal however to those that elicited feeding or gnawing Behaviorally Paul Miley and Baenninger [1971] found that nearly all male laboratory rats ...ean reliably to kill mice if they were kept on a cyclic food-deprivation schedule for two weeks and tested when hungry

There are several ways in which different species may interact in their natural habitats These include predation where one species may serve as food for the other competition in which both species feed on the same food resource (which may be a third species) and in which a zero sum situation may occur in times of scarcity A third type of interspecies relationship is parasitic in which members of one species serve as the host for the other Finally cooperative relationships such as mutualism or commensalism may occur in which members of both species ...enefit from one or both species working in their own interests These various re...lationships may not always be mutually exclusive in the long run as for example ...e predation of wolves on moose which seems ultimately to benefit the moose ...pulations by culling weakened or unfit members of the population [Mech 1966] ...ler [1956] found that 50% of caribou killed by wolves were crippled or sick ...ereas the incidence of such infirmities among the stragglers of caribou herds ...s estimated at 2% or less and even lower in the herds

Mouse killing by rats appears intuitively to be either a predatory or a com...itive relationship since it seems unlikely to be any of the others It is ...possible that the relationship of mice and rats outside the laboratory is a ...tral one in which the two species do not interact in any characteristic way ...mouse killing phenomenon would then be limited to the laboratory where it ...e clearly occurs in large numbers of rats It would therefore be of interest in its ...right but not for what it can tell us about ecological relationships of Rattus ...Mus or Peromyscus Nor would a knowledge of wild mice and rats from field ...ies be of much help in understanding mouse killing in laboratory rats ...alhoun [1962] reported no evidence of rat mouse interaction in his field ...y on Rattus in Baltimore In Ewer s field study [1971] of Rattus rattus in ...a she mentions attacks by rats on intruding mice toads moths and voles ... of which she assumed were treated as food because they were carried to ...nests

...an investigation of wild living mouse survival Berry Jakobsen and Triggs ...3] reported that weasels (Mustela nivalis) and stoats (M erminea) are the

only British mammals known to prey on mice These authors also claimed that birds are not important mouse predators on the basis of studies of droppings a mention that mice live in nesting sea bird colonies Berry et al do report that fewer mice are present if rats are living in the vicinity an observation frequently made by rustics in the United States as well Shenker [1973] reported that rat infestations are declining in London whereas either actual numbers or infestations have been increasing Whether this is a coincidental or causal relationship is uncertain according to Shenker Elton and Laurie [1954] reported the results of a annual sample census of rats and house mice in English corn ricks from 1943-19 They found that both populations had the same ranked preferences for available foodstuffs (wheat was preferred to oats which was preferred to barley) although rats ate approximately seven times as much as mice The percentage of rat infested ricks with more than 50 mice also present ranged from 33–70% whereas up to 9 of the rat infested ricks contained some mice Both populations showed population increases from November through March with mice continuing to increase through May Elton and Laurie report no specific behavioral interactions The implication of these findings is not entirely clear but there is little indication of predation by rats Rather successful competition for similar resources seemed probable with both populations living sympatrically In an environment where food was scarce a different picture might emerge with predation by rats on their competitors Rattus villosissimus was reported by Finlayson [1939] to prey on Mus musculus in Australia Dammerman [1929] reported that Mus were scarce where Rattus were present and in addition found evidence that rats ate mice when the opportunity occurred Nests of rats on Moray containing many mouse remains were reported by Gordon [1884] and Kalabukhov and Raevskii [1933] reported similar evidence from the Soviet Union

The picture is thus a confused one with evidence for and against predation on mice by rats or conversely for and against successful competition by two similar species The data are somewhat anecdotal and the older studies give little detail on methodological matters The census data reported by Elton and Laurie [1954] were collected by farm workers in England who were interested in the war effort they were not professional trained scientists and their powers of observation may have been deficient even though they were not testing pet scientific hypotheses Nevertheless the very confusion of the evidence is what would be expected if rats behaved in the opportunistic manner that characterizes mammalian predatory behavior The foregoing review buttresses the view that at least among mammals opportunity is the mother of predation

Mice (Mus and Peromyscus) are what Errington [1967] and other ecologists have called staple prey species They are preyed on by most predators at least some of the time every year in the USA a single weasel for example may consume 1 300 mice annually [Hall 1974] Occasional gorging on abundant prey is almost universal among predators as shown for example in the explanation of

grasshoppers in late summer on US prairies they are eaten by many mammalian and avian predators in vast numbers Local populations of mice which are vulnerably situated or have overproduced may be in the same situation even predator species that do not normally kill mice may do so under such conditions McCabe and Blanchard [1950] found that certain local populations of mice in their California field study were almost completely wiped out by weasels whereas nearby populations were not bothered by these predators at all

One variable that clearly causes shifts in prey selection is the relative abundance of alternatives Pearson [1964] studied carnivore–mouse interactions in a 35 acre grassland habitat near Berkeley Calfiornia Meadow mice (Microtus californicus) were the most abundant species with up to 190 individuals per acre Harvest mice (Reithrodontomys megalotis) were next most abundant with up to 50 individuals per acre In 1961 there was a population boom of Mus musculus which had been a rarity since 1948 in the locale The populations of all three species peaked in June 1961 and reproduction apparently ceased until the following spring The impact of several carnivore species (those suggested by Pearson were feral cats grey foxes raccoons and skunks) on this standing crop of prey was measured by systematically collecting droppings of predators Approximately 88% of 4 400 Microtus 33% of 1,200 Reithrodontomys and 7% of 7 000 Mus were eaten by predators by the spring of 1962 Rattus was not mentioned as a predator by Pearson who concluded that the predators showed a preference for Microtus an alternative may be that Microtus were the easiest to capture However as Microtus became scarcer increasing numbers of Reithrodontomys Mus and finally wood rats (Neotoma) were taken Tagging of mice in the center of the study area resulted in recovery (in carnivore scats) of 32% of Reithrodontomys 22% of Microtus and only 1% of Mus The major points of interest here are that prey selection was affected by changing abundance of alternatives and that Mus was not favored as a prey This could of course be due to their novelty in the sense that predators did not have a specific search image for Mus although their relative abundance and the long duration of the study make this explanation unlikely

In a later study in the same locale Pearson [1966] found that carnivores increased their Microtus consumption as the Microtus population increased Reithrodontomys were always preyed on less if Microtus were available

There are numerous examples of vertebrate predators learning to favor particular easily obtainable prey Virtually all vertebrate predators turn out to be omnivorous opportunists and there is no reason to think that rats which are well known for their catholic food choices should be any different Landry [1970] has discussed the order Rodentia as omnivores which may be carnivorous piscivorous and insectivorous as well as herbivorous as they were once thought to be Landry points out that Peromyscus leucopus in New Mexico normally lived on seeds but in Carlsbad Caverns fed on large crickets that dwelt in the caves The mice in the rest of the state probably also had the capacity for such

food choices and would have fed on crickets if such prey had been equally abundant

Given the possibility of opportunistic shifts in prey selection it seems entirely plausible that all rats should be capable of attacking killing and eating mice even though most of them normally do not Once the normal inhibition of killin prey is overcome in rats (perhaps by cyclic food deprivation as shown by Paul Miley and Baenninger [1971]) reinforcement of killing can occur whatever form that reinforcement may take [Baenninger 1974] and is sufficient to main tain killing in the future whether hunger is present or not Mice thus become potential prey for these rats

On the other hand the rat–mouse relationship may be a competitive one in which case mouse killing could be thought of simply as a matter of ridding the local habitat of a potential competitor for scarce resources In addition to the teleological implications of this suggestion a number of arguments may be made against such a view First territorial defense rarely results in permanent damage or death of the intruder Among conspecifics the intruder may be threatened or even attacked in general relatively little is known about territorial behavior when resident and intruder are of different species or genera Karli pointed out in 1956 that if laboratory rats are free to do so most of them will eat some of a mouse they kill Paul s recent research [1972] substantiates Karli s observations Territorial defense as it is generally understood may occasionally result in a resident ingesting an intruder but such an outcome *is not typical* Since mice can not leave a rat s laboratory cage the death of the mouse may be in some sense a laboratory artifact Rats are however remarkably tolerant of members of their own species and qualify as a contact species in Hediger s terminology [1950] Since most species tolerate members of other nondangerous species to an even greater extent than members of their own it would be surprising to find that rats were so intolerant of mice unless something more than territorial competition were involved

A second general argument against a competitive view of mouse killing is a statistical one Rats in their extra laboratory habitats are a broad niche species particularly Rattus norvegicus whose adaptability has permitted them to dis place the more specialized Rattus rattus in much of the world Rats are extremely adaptable to a wide variety of ecological niches in cities and in rural areas both with and without human habitation By contrast mice of the genus Peromyscus are narrow niche species ie their ecological requirements are limited and specific Wecker s work [1963 1964] on habitat selection in Peromyscus pro vides evidence of such specificity McCabe and Blanchard [1950] found a remark able degree of specificity in the ecological niches of three sympatric species of Peromyscus the three species in extra laboratory environments rarely met so complete was their ecological isolation The very fact that speciation had occurred in Peromyscus while it has not occurred in Rattus to nearly the same extent [illegible]

argument for the relative ecological isolation of Peromyscus and thus for the specificity of its requirements The house mouse Mus musculus is another matter It is much more likely than Peromyscus to be found sharing man s table as a commensal and thus potentially to be competing with Rattus However Mus has not been routinely reported around dumps slaughter houses and harbors Elton and Laurie [1954] did observe Rattus and Mus in the same corn rick much of the time but they did not report other species of mice at all

Based on speculations and very sketchy evidence therefore it appears that Rattus and Peromyscus are unlikely to meet often outside the laboratory although Mus may have greater contact with rats Peromyscus species appear to live in such specialized ecological niches compared to rats that the species as species are unlikely to be generally found as competitors local populations of rats and mice may compete temporarily but such interactions are unlikely to occur on regular basis This very segregation may reflect exclusion of mice from rat habitats or it may be the result of differing habitat preferences As Stoecker [1972] and others have shown these two possibilities are difficult to separate even with the aid of laboratory experimentation In both laboratory and field Stoecker found that two species of voles (Microtus montanus and M pennsylvanicus may exclude the other by behavioral interactions Baenninger [1973] showed in the laboratory that the success of Mus musculus in colonizing new territories may be due to its behavioral dominance over several species of Peromyscus Additional data on habitat preferences (if any) of Mus versus Peromyscus are necessary to determine the basis for segregation of the various species

In carnivores such as the Canidae [Fox 1969] and Felidae [Schaller 1972] attack and feeding responses appear to develop separately Juvenile play activities often look very similar to the prey-catching and/or aggressive responses of adults but do not become functional for predation until hunting experience with adults has been gained Only gradually does the integrated response chain of searching hunting/chasing capturing/attacking killing and feeding occur Given this developmental background it is not surprising that the separation of feeding and aggressive motivation can be demonstrated in mouse killing rats Berg and Baenninger [1974] demonstrated such a separation using the conditioned aversion paradigm When a mouse killing rat was allowed to kill and feed on a mouse and was then made sick with a dose of lithium chloride the rat stopped feeding on mice but continued to attack and kill them Giving LiCl to rats that killed but were not permitted to feed did not result in cessation of killing The fact that killing does not necessarily lead to feeding if appropriate experience with aversion conditioning is given does not invalidate the normal essentially predatory nature of the mouse killing rat s interaction with a mouse It may simply mean that rats are discriminating about what they feed on and less discriminating about what they kill

If rats are opportunists like most predators they may attack and kill a wide

range of potential prey Karli [1956] found that rats that killed Mus musculus also killed hamsters and other small rodents In unpublished observations I have found that mouse killing rats kill Peromyscus leucopus P polionotus P maniculatus bairdii as well as various strains of Mus musculus including several with varying pelage and even a hairless strain used in research on skin cancer Bandler and Moyer [1970] found that almost all laboratory rats attacked frogs and turtles about 45% attacked baby chicks but only 15% of their sample attacked mice There was a tendency for the rats to eat parts of the frogs and turtles but not the chicks and mice Johnson Desisto and Koenig [1972] found that rats kill cockroaches and frequently eat them The finding that attacks occur on a wider variety of prey than does feeding again supports the hypothesis that predatory behavior can be thought of as a sequence of acts that may be interrupted at any point between initial search and final feeding As has been amply demonstrated [Rozin and Kalat 1971] the laboratory rat s feeding choices are highly modifiable by their positive or negative dietary consequences When rats must first capture and kill their food some interesting differences emerge between the effects of consequences of killing and feeding as Posner [1973] has demonstrated He found that rats that were shocked for killing either mice or frogs stopped doing so and killed only the prey that was not associated with shock When rats were given a choice between killing mice and frogs and were permitted to eat the correct but not the incorrect choice there was no modification of their behavior in other words an aversive contingency affected prey choice but an appetitive contingency did not Since electric shock is a peculiar and perhaps unique stimulus the generality of this finding for predatory behavior is open to question but is of considerable interest

Mouse killing in rats appears to be different from other varieties of aggression as indicated by the fact that variables which produce other kinds of aggressive behavior do not reliably produce mouse killing Electric shock wh h causes rats to attack each other if they are together in a small cage does not normally cause non killer rats to attack mice [Myer and Baenninger 1966] Rearing rats in isolation does not result in a higher percentage of mouse killers [Myers 1969] Hormonal manipulations that modify the intraspecifi aggressive behavior of adult male rats do not change their propensity to attack and kill mice Pain isolation and hormonal manipulations typically result in increases in the frequency with which a gressive responses are emitt d [Baenninger 1974] their failure to modify mouse killing suggests that atta ks on mice belong to a different class of aggressive response Predatory behav or is a likely candidate Mouse killing by rats may be convergent with or analogous to predatory behavior in other species Like other predators a rat may attack a d kill a mouse and then eat it As discussed earlier in this paper this sequence of behavior is by no means inevitable and may cease at any of a number of poin s for a variety of reasons

An attack begun by a mouse killing rat on a small rodent amphibian or bird may ultimately be followed by feeding on the attack victim but that does not prove that the initial attack was predatory The attack may have occurred for quite unrelated reasons (intrusion on personal space irritable aggression or simply exploration of an interesting stimulus that may have some of the properties of an existing specific search image) The killing response may be aggressively motivated but feeding if it occurs at all may be motivated by hunger It is important to remember that the stimulus properties of the victim change in response to the predator s responses from a freely moving animal to a wounded perhaps immobilized victim to a still carcass There is no a priori reason to be sure that a predator s motives or responses should remain constant toward such a changing stimulus Plasticity of responses for internal reasons (ie brain stimulation) has been amply documented in laboratory rats by Valenstein Cox and Kakolewski [1968] Arguments about whether prey killing is aggressive behavior or not are somewhat beside the point since one is arguing about labels rather than behavior [Plotnick 1974]

The more important questions are the motivational circumstances (or antecedent condition ) and the ecological significance of attack behaviors in the life of a species in its laboratory and extra laboratory environments On the basis of the literature on predation reviewed here it appears that the story is not a simple one Feeding does not inevitably follow attack and killing and most predators are rather catholic in what prey they prefer to attack kill and eat Whether one is talking about rats attacking mice in the laboratory or hyenas attacking gazelles in the Serengeti Plain predatory behavior appears to be a matter of individual learning opportunities and motivational states This is not to deny that ecological models of predation are useful At sufficient distance all interactive behavior of living organisms can be described in terms of abstractions But the behavior of individual predators does not lend itself to nomothetic generalities

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AGGRESSIVE BEHAVIOR
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# ominance, Aggression, and the unctional Use of Space in nstitutionalized Female Adolescents

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This is a study of an institutionalized group of female adolescents observed for a nine week period These girls were observed to determine the characteristics of their domi nance relations and how in turn this aspect of their social environment was related to use of their physical environment Correlational analyses between observational and sociometric data suggested that dominance rank was based upon the frequency of being the recipient of a dominance act. Fewer dominance acts were initiated against higher ranking girls. Dominance ranking was not based upon frequency of initiating a domi nance act towards others. Higher ranking girls were the ones most frequently observed alone in their own bedroom Bedrooms were highly desirable areas used for grooming (eg, setting hair ironing clothes, putting on cosmetics, resting) as girls sought to gain popularity with the institution s male population Comparison of results with findings in similar studies on male adolescents suggest some tentative generalizations as to sex difference in dominance and territoriality

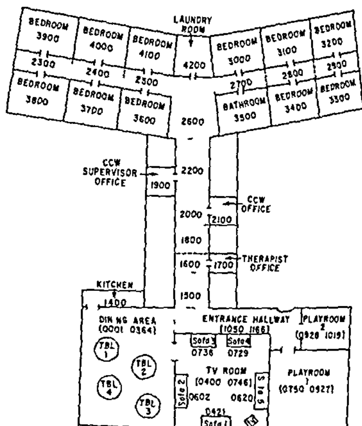
y words adolescents, dominance hierarchy territoriality sex differences

## TRODUCTION

Ethology studies behavior within a framework of biological evolution while thodologically stressing unobtrusive observation of naturally occurring events om this approach many important aspects of animal behavior have been eluci

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AREAS
1 DINING ROOM AND KITCHEN (0001 0364, 1400)
2 TV ROOM (0400 0746)
3 PLAYROOM 1 (0750 0927)
4 PLAYROOM 2 (0928 1019)
5 ENTRANCE HALLWAY (1050 1166)
6 CORRIDOR AND OFFICES (1500 2200)
7 BEDROOM WING (2300 4200)

Fig 1 Layout of cottage

this cottage before the start of this study Their IQ s ranged from 61 to 98 ($\bar{X}$ = 83 sd = 9.3) The cottage staff consisted of three men and seven women who worked in eight hour shifts of three or four staff per shift

## Procedure

The study period lasted for nine weeks Space use dominance and aggressive behavior of the cottage residents and staff were recorded by three tra ed obser vers placed in different areas of the cottage Observations were done Monday

through Friday during the hours of 15 30 and 18 30 These times were chosen because this was when most of the cottage residents were present in the cottage and were free to do what they pleased

Observations were recorded every 15 minutes in discrete and continuous forms Discrete data included information on location activity and social contact (if any) of each resident and staff member in the cottage Location data were recorded on preprinted maps which marked the cottage off into seven functional areas (see Fig 1) Special maps of areas 1–5 were further divided into 1½ foot by 2½ foot locations (not shown here) which were analyzed separately to determine locations which shared a high occupancy by one person If these were found they were combined into clusters of two to five locations which we considered as one territory In areas 6 and 7 location data were analyzed in general terms ie in which bedroom or office or in front of which bedroom or office someone was sighted Territorial behavior was defined as an individual s tendency to predominantly use one or a few places rather than using several places equally

In addition to discrete data observers continuously recorded as it occurred any dominance or aggressive behavior exhibited by the cottage residents or staff Continuous data included information on location participants involved (noting which participant was the initiator and which was the recipient of the dominance act) description of the dominance act as well as description of the response to it A dominance act was defined as a behavior directed at another individual which caused a physical insult (this was defined as an aggressive act) brought about withdrawal intimidated the other or limited the others behavior in general From a review of previously observed behavior repertoires [Esser 1970 Paluck and Esser 1971] and from preliminary observations of the cottage residents made by the first author five types of dominance acts were specifically observed for and the two last ones scored as aggressive acts

1) Verbal order eg A tells B 'Get me a cigarette
2) Verbal name calling eg A tells B 'This is the way you play this game ... You re a son of a bitch
3) Verbal argument eg A says to B You re wrong you do it this way A you do it like this B responds gets her way
4) Physical fight A pushes hits or otherwise physically assaults B eg A punches B in the stomach
5) Throwing object in order to inflict injury eg A flings a brush at B

Also each response to a dominance act was scored for whether it was 1) An immediate submission 2) A temporary counter argument which eventually lead to submission or 3) A retaliation which lead to the eventual dominance over the individual who initiated the dominance a t (a reversal)

Each observer was trained in the observational procedures during four two hour sessions These sessions provided a general introduction into observa-

other Thus would argue for the approximate accuracy of the assigned dominance ranking In general as could be expected the middle-dominant subgroup was the most unstable as they accounted for 12 out of the total of 14 dominance reversals observed Furthermore in only one case did a girl in the low dominance subgroup reverse the dominance initiative from a girl in another subgroup This was the result of an encounter between the highest ranking member of the low dominant subgroup and the lowest ranking member of the middle-dominant subgroup

### Frequency of Different Types of Dominance Acts

Nine of the 12 dominance acts displayed by the four high dominant girls consisted of verbally ordering another girl to do something for her there was only one aggressive dominance act exhibited by this subgroup In contrast while the 10 girls in the middle dominant subgroup also often displayed their dominance through a verbal order – this accounted for 23 of their 67 dominance acts while in 8 cases there was an argument or name calling – they showed a greater propensity for aggressive dominance acts They engaged in 26 physical attacks and exhibited 10 incidents of throwing an object at another in order to inflict injury As for the four girls in the low dominant subgroup four out of their five dominance acts were name calling none was ordering someone about

### Direction of Dominance Acts and Aggressee Behavior

In none of the 12 incidents in which a member of the high-dominant subgroup initiated a dominance act towards another girl was there a reversal In other words no girl ever successfully defended herself against the dominance of a high-dominant girl Of the 67 dominance acts exhibited by members of the middle-dominant subgroup 34 were directed to other members of this same subgroup and 12 of these were reversed As to the middle-dominant subgroup's 26 incidents of physical attack 16 were directed to girls in the low-dominant subgroup (none of these were reversed) and 10 were directed to the other middle-dominant girls (5 of these were reversed) Of the total of 84 dominance acts observed in the entire study 52 were directed towards a member of the low-dominant subgroup Members of the low-dominant subgroup immediately submitted 39 times They temporarily countered a dominance act 11 times (all initiated by members of the middle-dominant subgroup) and twice reversed a dominance act directed towards them (one by a member of their subgroup and once as mentioned by the lowest ranking member of the middle-dominant subgroup)

### Additional Correlations With Dominance Rank

Dominance rank was most significantly correlated with age ranking (rho = +0 69 P < 0 01) Other ranked variables such as IQ (rho = +0.24) frequency of

social interaction (rho = +0.33) and length of stay at the institution (rho = +0..9) did not correlate significantly with dominance rank The correlation between dominance rank and the rank of a girls most frequent social partner wa significant (rho = +0 41 $P < 0.05$) suggesting that girls generally interacted with others closer to their own dominance rank

## Territorial Behavior

To study the relationship between dominance rank and use of the physical environment we defined territorial behavior as an individual s use of predominantly one or a few places rather than being all over the place For each girl the percentages of her being in each location were calculated and ranked in descending order Since some locations used accounted for only a very small percentage of a girl s total observations we decided to show only those locations that accounted for the first 50% of each girl s total observations These data are presented in Table I

There was a general trend towards a positive relationship between dominance rank and territoriality (the predominant use of one or a few locations) Fifty per cent of the observations on each of three out of the four girls in the high-dominant subgroup (Nos 27 21 and 22) were accounted for by only three locations and each of these girls spent at least 35% of her total number of observations in her bedroom It took nine locations to account for 507 of the observations of the other girl (No 35) in this high-dominant subgroup 10 7% being the most she was observed in any location

Only two of the other girls stayed in three locations for 50% of her observations Both of these girls were in the middle-dominant subgroup For four girls it took between five and six locations to account for 50% of their total observations Also in contrast to the three out of four girls in the high-dominance subgroup who spent the largest percentage of their observations in their bedroom these six middle dominant girls tended to be observed most frequently on the sofas in the TV room

As for the four girls in the low-dominant subgroup it took between 7 and 12 locations to account for 50% of each of their total number of observations None could therefore be called territorial in terms of trying to occupy a space of their own In addition there were no instances of a girl losing a dominance act to an other girl outside her most frequent location while winning a dominance act over that same girl while in her most frequent location

## Dominance Acts and Area Usage

The frequency of dominance a ts was not evenly distributed throughout the seven areas as the summary in Table II shows For all residents the percentage of dominance acts observed in areas 2 and 7 was less than the average percentage of observations in those areas In all the other areas this relationship was reverse

TABLE 1 Patterns of Spatial Usage for Each Resident

| | [illegible] | [illegible] | [illegible] | RANK OF MOST FREQUENT LOCATIONS | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| HIGH DOMINANT | 1 | 27 | 3/52.6 | [illegible] | 0421 (7.1) | 0821 (5.7) | | | | | | | | | |
| | 2 | 21 | 3/53.7 | 3000 (43.0) | 3500 (5.4) | $T_1$ (5.3) | | | | | | | | | |
| | 3.5 | 22 | 3/53.2 | 4100 (38.1) | 0602 (12.8) | 0738 (5.2) | | | | | | | | | |
| | 3.5 | 35 | 9/52.2 | 0421 (10.7) | 3400 (9.2) | 1400 (7.6) | 0620 (8.2) | 3200 (5.7) | 0602 (5.0) | 3500 (2.8) | 2000 (2.8) | 0907 (2.3) | | | |
| MIDDLE DOMINANT | 5.5 | 39 | 5/50.4 | 0602 (19.1) | 3400 (12.6) | 0820 (8.1) | 1400 (5.3) | $T_3$ (5.3) | | | | | | | |
| | 5.5 | 31 | 3/54.1 | 0421 (22.0) | 0620 (20.1) | 0729 (14.0) | | | | | | | | | |
| | 7 | 37 | 7/50.6 | 0602 (11.7) | 3700 (10.9) | 0620 (9.3) | $T_1$ (6.8) | 0421 (6.5) | $T_5$ (3.2) | 4200 (3.1) | | | | | |
| | 8 | 23 | 8/52.3 | 4000 (14.1) | $T_1$ (10.0) | 3800 (9.8) | 0729 (4.6) | 0602 (4.0) | 4200 (3.6) | 3600 (3.1) | 0421 (3.0) | | | | |
| | 9 | 28 | 3/52.6 | 3200 (35.9) | 0421 (11.7) | 3100 (5.0) | | | | | | | | | |
| | 10 | 33 | 7/52.3 | 3100 (18.2) | 4100 (6.8) | 0421 (6.7) | 0738 (6.7) | $T_3$ (6.2) | $T_4$ (5.0) | 0620 (4.7) | | | | | |
| | 11 | 26 | 9/52.7 | 0729 (18.0) | 0620 (9.2) | $T_3$ (8.1) | 0738 (8.5) | 3300 (7.9) | | | | | | | |
| | 12 | 20 | 6/52.7 | 0431 (20.0) | 0602 (9.2) | 0738 (8.4) | $T_1$ (6.3) | 1400 (5.8) | 0620 (5.8) | | | | | | |
| | 13 | 24 | 6/50.6 | 0620 (17.2) | 0431 (13.3) | $T_2$ (4.7) | 0738 (3.6) | 0602 (3.6) | 3300 (3.3) | 3500 (2.5) | 0907 (2.5) | | | | |
| | 14 | 32 | 6/52.3 | 3800 (16.0) | 0421 (12.7) | 0620 (8.8) | $T_1$ (8.7) | 1400 (5.9) | $T_2$ (4.2) | | | | | | |
| LOW DOMINANT | 15 | 38 | 11/51.1 | 3800 (13.4) | $T_1$ (7.1) | 1400 (6.0) | 4200 (6.5) | $T_2$ (4.2) | 0908 (3.5) | 0421 (2.6) | 0602 (2.6) | 2000 (12.4) | 3600 (2.4) | 4000 (2.4) | |
| | 16 | 34 | 12/50.8 | 1400 (12.0) | $O_1$ (8.5) | 2000 (4.2) | 0802 (4.0) | $T_3$ (4.0) | $T_4$ (3.5) | 0738 (3.1) | 2100 (3.1) | 2200 (3.1) | 0827 (1.5) | 2500 (1.5) | 3600 (1.5) |
| | 17 | 30 | 7/52.8 | 0602 (14.2) | 3700 (12.2) | $T_2$ (6.0) | 0421 (4.8) | 0729 (4.6) | 0738 (4.4) | 0757 (4.4) | | | | | |
| | 8 | 38 | 12/51.1 | 1400 ( 8.1) | 0602 (6.0) | $T_3$ (6.0) | $T_2$ (4.5) | 3800 (4.0) | 0421 (3.6) | 2000 (3.5) | $T_1$ (3.0) | $T_4$ (2.6) | 2100 (2.0) | 4200 (2.0) | 0941 (2.0) |

1 [illegible]
[illegible]

| | Dominance Rank | Subject ID# | Frequency of Dominance Act | Location of Dominance Act | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Area 1 | Area 2 | Area 3 | Area 4 | Area 5 | Area 6 | Area 7 |
| HIGH DOMINANT | 1 | 27 | 1 | | 1 | | | | | |
| | 2 | 21 | 3 | | | | 1 | | | |
| | 3.5 | 27 | 4 | | 2 | | | | | |
| | 3.5 | 35 | 4 | 2 | | 1 | | | 1 | |
| | SUB TOTAL | | 12 (14%) | 4 (33%) | 3 (25%) | 1 (8%) | 1 (8%) | | 1 (8%) | 2 (17%) |
| MIDDLE DOMINANT | 5.5 | 39 | 4 | 2 | 1 | | | | 1 | |
| | 5.5 | 31 | 4 | | 3 | | 1 | | | |
| | 7 | 37 | 9 | 3 | 2 | | | | 4 | |
| | 8 | 3 | 4 | | | 1 | 1 | | | |
| | 9 | 8 | 4 | | 3 | 1 | | | | |
| | 10 | 33 | 7 | | | 5 | | 1 | | 1 |
| | 11 | 6 | 12 | 2 | 3 | 2 | 1 | | 2 | |
| | 12 | 0 | 9 | 6 | | | 1 | | | |
| | 13 | 24 | 7 | 4 | 1 | 1 | | | 1 | |
| | 14 | 32 | 7 | 3 | 2 | | 1 | | | 1 |
| | SUB TOTAL | | 67 (80%) | 22 (33%) | 15 (22%) | 10 (15%) | 5 (7%) | 1 (1%) | 10 (15%) | 4 (6%) |
| LOW DOMINANT | 15 | 36 | 2 | 1 | 1 | | | | | |
| | 16 | 34 | 0 | | | | | | | |
| | 17 | 30 | 2 | | 1 | | | 1 | | |
| | 18 | 38 | 1 | 1 | | | | | | |
| | SUB TOTAL | | 5 (6%) | 2 (40%) | 2 (40%) | | | 1 (20%) | | |
| | TOTALS | | 84 | 28 (33%) | 20 (24%) | 11 (13%) | 6 (7%) | 2 (2%) | 11 (13%) | 6 (7%) |
| | Mean % of Observation in Each Area | | | 21.2% | 8.8% | 8.8 | 3.7% | 1.7 | 5 | 9.7 |

### Activities

Data were collected on the activity each girl was engaged in at the time she was observed These data were tabulated into 13 categories (0–12) When a girl s activity was not visible to the observer (eg when a girl was behind closed doors) the activity category unknown (No 0) was recorded The other activity categories included the following 1) talking 2) walking 3) watching TV 4) object involved (eg sewing reading) 5) eating 6) sleeping 7) cottage task (eg sweeping floor clearing dinner table) 8) playing a game 9) watching a game 10) chasing someone 11) grooming and 12) participation in a therapy session

The percentage of observations of the unknown activity provides a useful measure of visibility Highly visible girls would be those most often observed in the public spaces where they would be visible to other girls and staff as well as to observers Those low in visibility would be those girls who located themselves in private spaces Results showed that those higher in dominance rank were less visible both in solitary behavior (rho = +0 51 $P < 0.05$) and in dyadic social interaction (rho = +0 46 $P < 0\ 05$) as compared to lower dominant girls

Lower dominant girls were observed more often than higher dominant girls watching TV (rho = –0 55 $P < 0\ 05$) Also a near significant negative correlation was found between dominance rank and frequency of participation in games

## DISCUSSION

The results of this study indicated that dominance hierarchy and territoriality can provide a framework within which to account for a significant part of the behavior observed in group living adolescent females A dominance hierarchy based on the criteria of the least number of times a girl was the recipient of a dominance act seemed to structure the data in an orderly way and was highly correlated with staff's ranking of girls This passive criterion of dominance as opposed to one that would define the higher ranking girl as one who initiated more dominance acts could have resulted from this being a stable population that had been living with each other for at least six months prior to the beginning of this study With little changeover in population the active display of dominance by high ranking girls may not have been necessary – their rank was already established *

However this was not entirely the case since at a meeting with the cottage staff at the end of the study they indicated general agreement with the aforementioned dynamics but pointed out another factor involved something they called the chain of command " It was the staff's feeling that at times the three highest ranking girls (based on the behavioral data) did actively exhibit their dominance but only indirectly These highest ranking girls would instruct girls of middle-dominant rank who acted as their "lieutenants" to beat up or in some way intimidate specifically identified group members These instructions were usually given late at night not during the observation period

The dominance hierarchy based on the behavioral data accurately predicted the direction but not the frequency of dominance interactions* Given this finding it seems reasonable to ask not how the hierarchical structure functioned to minimize conflict between girls (frequency) but how each girl s dominant/submissive behavior (direction) functioned to maximize her rank or minimize the loss of her rank [Parker 1974 Smith 1974] and to ask furthermore how such behaviors were the results of and happen as organizing events in the same hierarchical structure

As observed in monkeys [Deag 1977] individuals in different parts of the hierarchy (high middle low) differed in the behavior used to maintain or increase their rank and hence their fitness Girls in the low-dominant subgroup were the recipients of most of the dominance behavior observed in the cottage but hardly ever initiated such behavior The low-dominant subgroup made up only 22% of the population but received 62% of all dominance initiatives They had little opportunity to increase their rank but did however minimize their loss of fitness by immediately submitting 75% of the time

The only times girls in the low-dominant subgroup tried to counter a dominance act was when the initiator was of a rank below 11 ie when a girl clearly belonged in the lower half of the hierarchy When girls in the low-dominant subgroup initiated dominance acts (five times) they usually used verbal name calling

It appears *significant to us that never* was a dominance act directed to any girl in the high-dominant subgroup Girls in the middle-dominant subgroup directed 50% of their dominance acts towards the members of the low-dominant subgroup and 507 to members of their own subgroup Dominance acts which were directed internally *within this subgroup* can be viewed as attempts to compete with peers in order to maximize a ri e in rank within the subgroup while remaining subordinate to the high-dominant subgroup until such time (even if we never observed it) as they could challenge them However within the middle-dominant subgroup there was a *relatively* high probability (36%) that the initiator of a dominance act would actually *lose Thus in turn* can easily release the desire for more dominance acts as was also observed in the recurrence of most fights in the middle-dominant subgroup by Esser et al [1965] Sundstrom and Altman [1974] and Hold [1976] also report on unstable middle-dominant subgroups in studies with male adolescents and preschoolers of both sexes respectively The instability in the relations *between* girls in the middle-dominant subgroup could *contribute to their desire* to initiate dominance acts towards girls in the low-dominant subgroups in order to minimize their "loss of status when losing many *dominance interactions* within *their own subgroup*

It is noteworthy that No 26 *the most* assertive girl ( he initiated 12 dominance acts) was the only girl of the middle-rank subgroup not observed in social interactions with any of the four high-dominant girls. *This* observation suggests that benefits accrue to those who are able to form bonds with high-dominant individuals [Weisbrad and Goy 1976] Inter acting with a hi h-dominant individual may impl citly display dominance albeit tempor ... ual assertion.

The girls in the high-dominant subgroup were never the target of a dominance act relatively infrequently initiated any dominance acts and only once engaged in a physical attack This observation that high-dominant individuals were not necessarily the most aggressive individuals in the group has also been reported for human adolescent males [Savin Williams 1977] and for female baboons [Rowell 1966] Japanese macaques [Kawaii 1958] and rhesus macaques [Sade 1967]

As to the similarities of the girls behavior with that of adolescent boys [Esser 1973 Sundstrom and Altman 1974] our data also showed a positive relationship between high dominance and territoriality

With regard to spatial patterns the girls in the high-dominant group were observed most often alone in their bedroom So we must ask how this contributed to their fitness Along with low visibility the bedroom offered girls in the high dominant subgroup a place to sleep rest groom and protect their clothes and cosmetics from vandalism which was a frequent occurrence with many of the other residents * In effect it gave the high-dominant girls the opportunity to enhance their attractiveness vis a vis the resident male population at the St Cabrini Home and thereby in a very real sense increased their fitness † In fact it was reported to the investigators that traditionally the highest dominant boy at the St Cabrini Home (as defined by staff) always goes with the highest dominant girl In addition we learned that one of the first experiences of the new resident who came into the cottage during this study was to be called into the bedroom of the second ranking girl The newcomer was then told by her and by the girls who ranked first and third what boys she could not look at and what would happen to her if she did she would get hers High-dominant girls were otherwise known to prevent other girls from pairing with high-dominant boys

In terms of spatial usage for the high middle and low-dominant subgroups, the bedroom – a privacy retreat [Bakker and Bakker Rabdau 1973] – was where the high-dominant girls were observed most frequently Even though girls No 27 and No 28 who were twins shared a bedroom (location 3,200) during part of the study they were almost never observed in that bedroom at the same time Privacy in this group might have been preferred because 1) It offered a time and place in which a girl could attend to herself in order to enhance her

* It is interesting to note here that on every bedroom door except on the doors to the bedroom of the girls who ranked first and second there was some "territorial saying" for example Private Keep Out Or If you read this sign you re too close The most dominant girls perhaps did not need to make such explicit requests they were "granted" privacy

† In this regard the significant correlation (rho +0 69 $P < 0\,01$) between rank and age might relate to the older girls (age 16 17) being in their reproductive prime as compared to the younger girls (age 14 15)

attractiveness to the boys and 2) Based on their life experiences these girls are extremely suspicious distrustful and resentful of others Thus being the case the high-dominant girls who could obtain such absolute privacy did so Middle dominant girls also obtained some sort of privacy in the sense that they were observed most often on sofas in the TV room where they watched television and did not interact socially Hence for girls in these two dominant subgroups a positive relationship between dominance and territoriality existed

The boys in the Sundstrom and Altman study [1974] were of a similar background to these girls and therefore it probably can be said that they too were suspicious distrustful and resentful of others Why then did they while also showing a positive relationship between dominance and territoriality prefer the pool room a public and social space to other areas of their cottage? At least two possibilities exist First as Coleman [1961] reports adolescent boys are more interested in competitive games than adolescent girls and mainly gain their status from such intragroup activities On the other hand adolescent girls gain status through their intergroup relations with boys This explanation must be tempered though by the fact that these sex differences refer to modal behavior and do not imply that distributions of male and female potentialities do not overlap A second explanation for the finding that the boys preferred a public social activity oriented space whereas the girls seemed to prefer the more private area of their own bedroom is that the cottage design was different in the two groups The boys bedroom area was barracks style where the beds were lined up in one large room the girls in our study lived two in a room In a study of boys between 9 and 14 years old Esser [1973 p 136] found that 36% of fights were territorial in a bedroom type cottage However it remains for future research to ascertain if indeed boys living in private or semiprivate bedrooms would prefer that area over more social activity-oriented areas available to them Girls in the low-dominant subgroup were observed most often at locations in the dining room and kitchen which were least private and can be called public and social spaces This can be partially explained by noting that the least dominant girls might have looked for protection from staff in these areas as Esser [1970 p 38 and reference by Grant p 59] in past studies has described how association with the staff power structure may enhance the status of a low-dominant individual

This also helps explain why the least desirable areas (kitchen dining room and hall) were the ones where a disproportionally high percentage of dominance acts occurred This finding in our study might just be an artifact of our definition of a dominant individual – low-dominant individuals are the ones most often dominated and observed in what we called the least desirable areas Although when one looks at the dominance/submissive behavior data for the girls in the low-dominant subgroup and compares the ratio of the percentage of the total number of times they were dominated in each area with the percentage of their

observations in each area one finds that in the bedroom area this ratio is smaller than in any other area This might be because the high-dominant girls often had their bedroom door closed and did not know that other girls were present in the area However another plausible interpretation of this finding is that dominance acts occur at a disproportionately high rate in least desirable areas because these areas are also less socially organized Only future research can elucidate this point

In conclusion we would like to speculate on how our interpretation of the results of these comparable studies of socially maladjusted adolescent males and females extends to the following finding It has been reported [Kaplan 1976] and it is the authors impression from their acquaintance with a number of residential settings charged with the care of this type of population that the staff in such institutions finds it much more difficult to cope with the aggressive antisocial behavior of girls as compared to that of boys If as we have stated earlier boys gain status from intragroup activities and status in turn gives one the ability to lead others in the group as opposed to girls who gain status from intergroup relations with boys then the lack of such *internally* group-directed motivation for dominance could result in the girls having no reason to be more subtle and diplomatic in their social relationships with others in their group Instead their behavior is often primitive and impulsive This tendency towards explosive behavior was shown in a study of aggression conducted by King and Deutsch (in preparation) at a home for juvenile delinquents in New Jersey They report that over a four year period girls were involved in aggressive episodes which were severe enough to result in the separate isolation of the participants in a locked unit away from their cottage at a rate two and a half times greater than the boys at that institution

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AGGRESSIVE BEHAVIOR
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# Mediating Factors in Chick Social Pecking II Effects of Exposure to Movement

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Unfamiliarity with movement may lead isolated chicks to respond aggressively when tested with live moving conspecifics. This hypothesis was tested by comparing the number and locus of pecks by isolated chicks to a stationary or moving model of a chick and to a live chick In a second test of the hypothesis chicks that viewed a moving object during isolation and chicks isolated without movement were tested with a live con specific and their number and locus of pecks were compared Neither experiment supported the hypothesis Movement alone failed to excite aggressive pecks and prior experience with *movement failed to suppress aggressive pecks*. In the first experiment isolated chicks treated the live testmate more aggressively than the moving or stationary model. In the second experiment aggressive pecking of chicks was unaffected by prior experience with *movement These findings* do not support the hypothesis that movement excites aggression in isolated chicks. Nonetheless the results focus attent on on the generally neglected problem of emotional and motivational states produced by isolation.

words chicks mechanical chick model isolation movement pecking

## RODUCTION

Our present purpose is to study the effect of movement on the aggressive ing of isolated chicks Aggressive behavior is elicited by movement in mam [mice Lagerspetz and Portin 1968 Cairns and Scholz 1973 Connor and ls 1977 rats Albert and Galef 1973 Blanchard et al 1975 and rabbits /towycz and Hesterman 1975] and fish [*Betta splendens* Thompson ] hence information on birds is important to the comparative psychology

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parable patterns and levels of social pecking in chicks with or without brief prior visual and tactile contact with broodmates [cf Rajecki et al 1976 Rajecki et al 1977] The birds were not sorted by sex each was marked with a felt pen for identification

Individual chicks were placed in 22 5 X 17 5 X 17 5 cm metal cages modified with clear plexiglass rear walls The cages were equipped with eparate petri dishes filled with water and chick starter A 40 watt bulb installed on the front mesh wall of the cage illuminated and heated the unit to 30° C The individual cages were arranged in groups of 12 in 105-cm high and 98 cm wide racks

Some chicks were given a view of a moving object through the clear wall of their home cage The object was a windmill like arrangement of eight 46-cm long blades Each blade had a width of 1 cm When activated by an electric motor the blad s turned in a clockwise direction at 10 rpm This bladed device was placed within 10 cm of the clear walls of the rack of cages with the hub of the blades aligned with the center of the rack When the blades were activated by a timing circuit the 40 watt cage lights were extinguished and a bank of twelve 40 watt bulbs located behind the blade were illuminated When the blades were deactivated the bulbs behind the blades were extinguished, and the cage bulbs were illuminated This lighting procedure was used to increase the likelihood that the subjects actually observed the moving object For control chicks exposed to a nonmoving object the switching of the lights was yoked to the schedule of the experimental birds The difference between conditions was that these control chicks were given a view of eight blades that never moved

Test apparatus Approximately 48 hours after a chick had been isolated it was tested for social pecking in a 22 5 X 17 5 X 17 5 cm metal cage Some chicks were tested with a ceramic model that was mounted on a 7-cm plastic base The model and a live chick are shown in Figure 1 We chose to use a chick like configuration to assess the influence of movement on aggression during tests since most studies in this area have pitted hatchlings against their broodmates Use of the configuration shown in Figure 1 allowed us to categorize pecks at the model in terms of locus (head body foot) which makes our data comparable to those from earlier researchers

For a chick assigned to a stationary model condition the model was securely anchored to fittings in the mesh floor of one of two test cages For a chick assigned to a moving model condition the model was disconnected from the fixed fittings in one cage and was mounted on a 7-cm compression spring (made of -gauge spring steel) in an adjacent cage The spring was installed through an opening in the cage floor and was connected to an axle powered by an electric motor The motor turned the spring (and the model) in a clockwise direction for three second periods interspersed with three second pauses The model completed about 5° of turn per second The spring arrangement made the model appear quite motile to the human eye The movement created by the mo



Fig 1 Photograph of a live chick with the mechanical chick model employed in Experiment

caused the model to jiggle perceptibly and any handling of the cage (such as would be required for the installation of a subject) or pecks by the subject used the model s head to rapidly oscillate through a 10–20° arc

) During tests the chicks pecking responses were recorded on a multichannel operations recorder Pretest estimates of interobserver reliability proved satis factory The chick s distress vocalizations were also recorded on the operations recorder chart via an amplitude-sensitive voice key [see Rajecki 1974]

**Procedure and design** In Experiment 1 the influence of target movement on isolates social pecking was assessed in two separate blocks of testing The proce dures over the two blocks differed in several respects so for clarity s sake they will be labeled Experiment 1A and 1B

The basi design of Experiment 1A was a 2 X 2 factorial with a sample size of 15 isolates in each cell The first factor represented the stationary and moving model conditions described above The second factor reflected whether or not subjects experienced movement in the home cage during isolation Half the iso lates could see the moving blades through the transparent wall of the cage for a five-minute period every half hour during their two days of isolation The other isolates viewed a set of nonmoving blades

While it is clear that in this paper the emphasis is on the effects of isolation a number of subjects that had been reared in pairs were also tested These socially reared birds provided another point of comparison against which to assess the influence of the treatments given to isolates Twenty four pairs of socially reared birds were tested as yoked controls in the 2 X 2 design Ea h social chick was run individually its cagemate remained in the home ca e during that test

For a test a chick was carried to the apparatus in its home cage (or in a spare cage if it was a socially reared bird) and was placed in the test cage facing the model at a distance of no more than 7 cm Tests in this study lasted 5 minutes

In Experiment 1B all the chicks (n = 44) were reared in isolation for 48 hours in the absence of moving objects The point of Experiment 1B was to a sess the chick s reactions to a moving model (above) in comparison to their reactions to a live chick All chicks in this subexperiment were tested with both the moving model (*individually*) and with a live chick (some other isolate) The chick–chick tests took place in an otherwise empty cage The birds were placed in the cage simultaneously facing one another at a distance of 5–10 cm Half the chicks en countered the model first (chick to model sequence) Tests in this experiment generally followed the procedure of Experiment 1A but were reduced to a dura ion of 2.5 minutes because of a laboratory scheduling constraint The two tests chick–model test or chick–chick test) of any given subject were separated by n interval of 5–10 minutes

*esults*

Experiment 1A The pecking data from Experiment 1A were cast in a 2 X 2 2 X 4 analysis of variance These factors represented (in order) isolated versus cial rearing movement versus no movement during tests movement versus no ovement during rearing and peck locus (the model s head body feet or the st cage) Only two of the 15 possible comparisons from this analysis were signi :ant First there was a strong effect for the model s movement The average imber of all types of peck per minute during moving model tests was 1.37 com red to an average of 0 38 for the stationary model ($F$ [1 75] = 14 22 $p <$ )1) Second peck locus was a source of variance ($F$ [3 225] = 4 64 $p < 0\,01$) ie overall average pecks per minute at the model s head body and feet were spectively 0 92 0 40 and 0 86 An average of 1.31 pecks per minute were ected at the test cage

An analysis of distress vocalizations in Experiment 1A revealed that only the cial versus isolate rearing comparison proved to be significant ($F$ [1 75] = 10 $p < 0\,05$) The socially reared chicks emitted a per minute rate of 4 83 ls while the corresponding rate for the isolates was 15 03

Experiment 1B The pecking data from this subexperiment were analyzed in X 2 (X 4) design that included test sequence (model to-chick versus chick to odel) tests (test 1 versus test 2 which for appropriate subjects represented ck–chick or chick–model tests) and peck locus (head body feet cage) The an number of responses by both members of test pairs was considered the unit analysis because in the chick–chick tests the observations were not independent One pertinent comparison that proved significant was the interaction between test sequence and test fa tors ($F$ [1 20] = 9 82 $p < 0\,01$). The per minute rages of all types of pecks in the model to-chick sequence were 1 64 and 3 ich indicates that chicks pecked more at one another than at the model

**TABLE I Average Number of Pecks Per Minute by Isolate Chicks as a Function of Test Conditions in Experiment 1**

| | Subexperiment | | | |
|---|---|---|---|---|
| | Experiment 1A | | Experiment 1B | |
| Response | Stationary model | Moving model | Moving model | Live chick |
| Head peck | 0 32 | 1 72 | 2 44 | 6 56 |
| Body peck | 0 10 | 0 45 | 0 49 | 0 68 |
| Foot peck | 0 29 | 1 23 | 0 67 | 1 85 |
| Cage peck | 0 84 | 2 60 | 3 44 | 1 49 |

the chick–chick test followed the chick–model test The source of the interaction under scrutiny becomes clear in the overall peck means for the other sequence the chick to model test order Those respective averages were ? 15 and 1 87 Here it is again evident that chicks pecked more at one another than at the model even when the chick–model test followed the chick–chick test

Further peck locus was stable (like overall peck rate was stable) regardless of test order ($F(3\ 60) = 15\ 33$ $p < 0\ 01$) The locus and average (per minute) rate of pecks the subjects aimed at the moving model and at one another a e summarized in Table I The data from the isolate chicks of Experiment 1A are also presented in Table I for reference It can be seen that the moving model condition of Experiment 1B generally replicated the equivalent condition from Experiment 1A and that in terms of the pattern of head and cage pecks the live chick condition did not closely resemble any of the results obtained with the model To express the difference between the model and the chick conditions another way of the total sample of 44 animals in Experiment 1B fully 41% failed to deliver pecks to the head of the model whereas only 2% did not peck at the head of the live testmate

The only significant effect for distress vocalization in Experiment 1B is that chicks gave more calls in the first test ($\bar{X} = 15\ 81$) than in the second test ($\bar{X} =$ 7 37 $F(1\ 20) = 5\ 87$ $p < 0\ 05$) This finding will be taken up in a later section

## Discussion

It seems evident from the pecking data that the artificial chick model was not the equivalent of a live chick Pecks at the head of opponents have been taken as one manifestation of an aggressive disposition in isolate hatchlings (cf Rajecki et al 1976 Rajecki Nerenz et al 1977) but isolates (and socially reared birds) in this study showed relatively little inclination to peck at the head of the stationary model The movement of the target did increase the rate of pecks in Experiment 1A but chicks were more likely to peck at the test ca than at a

particular point on the model (see Table 1) Moreover while the isolates in Experiment 1B reacted in the expected fashion when they encountered a live conspecific they did not respond to the model as if it were a chick even when chick–model tests followed chick–chick tests Again movement of the model elicited pecks in Experiment 1B but the model s head was no more likely a target than was the test cage

To the experimenter s eye the model was quite realistic (see Fig 1) but it seems it was le s so in the eyes of the subjects even when it was moved There fore the hypothe is that just any movement during tests is the essential factor in chick social pecking receives little support Apparently the interaction between live isolate is more complicated than we first believed The data indicate that simple configuration and gross movement are not the factors involved in eliciting hatchlings aggressive behavior This finding provides the basis to recommend more refined tests that perhaps should include the features of fine movement vocalizations tactile variations and retaliatory pecks

Similarly the hypothesis that the experience of nonconspecific movement during i olation would influence social pecking received no support The authors were somewhat surprised at this outcome given the behavior of the isolates when exposed to the moving object in the rearing unit Casual observations found the isolate chicks pu hing vigorously against the clear wall of the ca e when the object was activated The impression was that the chicks were motivated to approach the moving object Further when the object was deactivated many isolates emitted distress calls These sorts of responses were not seen in he nonmovement control birds Unfortunately Experiment 1 had no provision or the regular measurement of chicks reaction to the moving object Another otential difficulty is that all chicks in Experiment 1 were tested outside the ome cage which means that the chick had to be separated from the object for test This separation may have disrupted the behavior of these particular sub cts [see Rajecki Suomi et al 1977] and any differential effect for rearing may ave been masked These problematic points were eliminated in a second study ncerning movement seen from the home cage and intersubject pecking

## XPERIMENT 2

### ethod

Subjects and housing The subjects were a fresh batch of 48 White Leghorn icks procured and housed as in Experiment 1 Half the subjects were exposed the home cage) to the rotating object employed in the first study However this experiment the blades were activated for 25 minutes each half hour in ad of the 5 minutes per half hour provided in Experiment 1B The duration of exposure was increased to help insure the impact of the treatment Control

subjects were exposed to a set of nonmoving blades Because of observer schedules half the subjects were tested after 24 hours in isolation and the remainder were tested after 48 hours *

Procedure and design In this study birds that had been isolated with movement were pitted against control chicks isolated without movement Half the tests took place in the home cages of experimental (movement) chicks and half the testing was done in the cages of the control (nonmovement) birds Tests lasted 5 minutes during which time the object was either moving or stationary outside the appropriate rearing units For a test one subject was transferred by *hand to the home cage of its opponent The bird in the home cage* was not handled but the opening of the cage did interrupt ongoing behavior Observations were made through the mesh front wall of the cage

Pecking data were obtained as in Experiment 1 but in the current study vocalizations were coded by ear [after Rajecki Suomi et al 1977] because the voice key could not distinguish between individual birds An additional measure was recorded that reflected the birds reaction to the moving and nonmoving objects It has already been noted that certain subjects pushed vigorously against the clear wall of the home cage apparently in an attempt to approach the moving object The observer (one per bird in these tests) recorded the frequency and duration of these pushing episodes by depressing a button on the operations recorder for the length of an episode The recording chart was calibrated in 2 second intervals per minute in which the phenomenon occurred A subject's score on this variable could range from 0–30 per minute

In sum the basic design was a 2 × 2 factorial with factors representing movement or nonmovement during social isolation and test location in either a movement or nonmovement home cage

## Results

For the analysis of these data the responses of individual subjects were treated as independent observations This procedure was necessary since subjects from the two independent treatment conditions were involved in each test To use an average score for these pairs would obscure any and all treatment effects

The data from the cage push measure were assessed in a 2 × 2 design representing the two levels of the rearing and testing conditions The average ra es of this response per condition are provided in Table II There were more pushi responses made by the movement reared birds than by the control subjects ($F$ [1 44] = 22 36 $p < 0.01$) and there were more of these responses under the movement test condition compared to the stationary condition ($F$ [1 44] = 9 61 $p < 0.01$) Finally there was an interaction that indicated the most cage pushing by movement reared birds under the movement test condition ($F$ [1 44] = <00 $p < 0.05$) Clearly there is evidence that the experimental (movement) chi ks were aware of the moving object as indicated by their behavior during tests

* Previous research suggests that periods of isolati n ranging from 24 7 ho rs ha e ... an equal influence on chick social pecking (Rajecki et al 1976)

TABLE II Average Responses Per Minute by Chicks as a Function of Test and Rearing Conditions in Experiment 2

| Response | Test condition | | | |
|---|---|---|---|---|
| | Cage with movement | | Cage without movement | |
| | Chick isolated with movement | Chick isolated without movement | Chick isolated with movement | Chick isolated without movement |
| Head peck | 5 97 | 3 53 | 5 17 | 7 17 |
| Body peck | 1 77 | 0 93 | 0 52 | 1 27 |
| Foot peck | 1 27 | 0 70 | 0 08 | 0 48 |
| Cage peck | 0 18 | 0 50 | 0 38 | 0 18 |
| Cage push[a] | 7 47 | 0 66 | 2 18 | 0 00 |

[a] The range of this measure is 0–30 scoring units per minute

In terms of the peck responses, a 2 X 2 (X 4) analysis (reflecting rearing and test conditions and peck locus) revealed no overall differences between the movement and nonmovement test conditions (F = 0 01 n.s ) and no differences between chicks from the movement and nonmovement rearing conditions (F 0 03 n.s ) However peck locus proved to be an important source of variance with the current isolates directing most of their pecks at one anothers heads (F [3 132] = 51 41 $p < 0\ 01$) Average rates of pecks by condition are presented in Table II Although there were absolutely no main effects for rearing or test conditions an interesting interaction between these variables approached conventional levels of significance Inspection of Table II reveals that chicks from both rearing conditions tested in their home cage had a certain advantage over the newcomer in terms of overall pecks (F [1 44] = 3 78 $0\ 10 > p > 0.05$)

The results of an analysis of distress vocalizations revealed a kind of separation effect Three of the four conditions had rates of distress vocalization of fewer than one per minute The exception to this low rate came from moveme t reared birds tested in the nonmovement condition These chicks gave an avera e of 14 45 calls per minute which resulted in a significant test X rearing condition interaction (F [1 44] = 6 49 $p < 0\ 05$)

## Discussion

The results of Experiment 2 are consistent with those of Experim nt 1A Both studies failed to provide evidence that the provision of a moving obje t during social isolation influenced the reactions of chicks to live conspecifics This negative finding is especially impres ive in Experiment 2 given the larg amount of exposure in that study (50 minutes per hour) and the good internal evidence that chicks from the movement rearing condition were aware of the presence or absence of the object s movement

Another interesting finding from Experiment 2 is that chicks as young as 4- 48 hours have a home advantage in social pecking tests It should be mentione that the differential advantage in these tests might have been an artifact of th procedure due to a) the handling of the newcomer prior to tests b) a separa n effect for the movement reared birds tested in nonmovement cages or c) a dis traction effect for the nonmovement reared birds tested in the presence of th rotating object Still home-cage (or secure-base) effects are on record for ch ks in related tests where these possible artifacts were not involved [cf Raje ki et al 1978 Wilson and Rajecki 1974] and until contrary information is availabl the current results can be counted as evidence for the impact of fam liarity the test situation on success in aggressive encounters

## GENERAL DISCUSSION

The studies reported here shed light on the phenomenon of isolation-induced social pecking in domestic chicks Experiment 1 showed that there is a c

siderable difference between isolate chicks reactions to an animated mechanical model and their reactions to live conspecifics Even though the model was fairly realistic in configuration and was made motile it did not elicit the pattern and rate of pecks seen in encounters involving two chicks The pattern of a high rate of head pecking and a low rate of cage pecking among isolate testmates was confirmed in Experiment 2 These findings suggest that there may be a species specific cue (or combination of cues) for aggression involved in some aspect of the physical appearance or behavior of a live chick. The hypothesis that the simple movement of a target is responsible for the head pecking of isolates was not supported The moving model was arranged so that its head region showed the greatest amount of oscillation and the painted eyes of the model provided the starkest figure ground contrast in the test unit (at least to the human eye) Even so in both tests involving a moving model the model was no more likely to receive pecks than was the test cage Chicks therefore seem very sensitive to some (as yet unspecified) feature of the behavioral topography of broodmates *

The results of Experiment 2 failed to support the hypothesis that a view of a moving object during social isolation would reduce social pecking in tests The experimental subjects in that study received almost continuous visual stimulation by a moving object A portion of the object passed by the clear plastic walls of their cages 500 times an hour every hour they were in social isolation The cage pushing means in Table II and the distress call measure reported on a previous page confirm that the chicks were aware of the presence and the absence of the movement of the object Nevertheless the pecking behavior of the stimulated chicks was indistinguishable from that of control birds that were reared in the absence of movement In the authors view the pushing and vocal behavior† may provide a clue as to why the experimental animals reacted with social pecking in tests with a conspecific despite the fact that they received considerable visual stimulation while alone That is a large part of the isolate s motivation to peck at a conspecific may be a result of the very stress of isolation Research in our laboratory has indicated that visual and tactile isolation produces distress vocalization and other disturbance reactions even in chicks that had never seen or felt another chick [Rajecki Suomi et al 1977] Therefore the typical isolation procedure may produce an animal in a chronic state of some unpleasant

*This point is illustrated in a study of infectious disease in fowl When Andrewes [1960 p 98] placed healthy chicks in a situation that contained only chicks infected with Newcastle disease it was found that under this circumstance the healthy birds would congregate near the infected group However when healthy chicks were placed in a situation that contained both infected birds (at one end) and uninfected birds (at the other end) the subjects collected near the normals Apparently the subjects in the Andrewes study could recognize some aspect of the normal behavior of conspecifics and found this behavior more attractive than the behavior of diseased counterparts. This finding seems to indicate that even very young chicks can make relatively *fine* discriminations between normal and other-than-normal movement of avian configurations.

†In general however results of the current studies add to the impression [cf Rajecki et al 1978] that there may be no predictable relationship between pecks to the head and distress calls at least for chicks under these circumstances.

emotion When a bird in such a condition encounters a target that elicits social pecks (such as a live conspecific) the chronic state of motivation may heighten the general tendency to peck

The idea that emotional reactions to isolation per se may energize social pecking in later tests seems to fit many of the findings in this literature First isolation and separation are known to produce negative emotional reactions in precocial hatchlings [Rajecki Suomi et al 1977] and do lead to aggressive responses in these birds (eg Hoffman et al 1974 Rajecki et al 1976] Second the provision of an imprinting object that is accessible to the isolate drastically reduces conspecific aggression even though the imprinting object bears very little resemblance to the isolate s species mates [Hoffman et al 1975 Rajecki et al 1978] Since chicks reared in pairs show none of the day to-day emotionality evidenced by isolates (see Rajecki Suomi et al 1977] it seems reasonable that hatchlings reared with a surrogate would be less upset than hatchlings reared alone Finally the provision of a visible animated object that cannot be approached (Experiment 2 above) does not reduce conspecific aggression probably because the repeated frustration of approach attempts causes an adverse and chronic emotional reaction in chicks

In sum the hypothesis advanced in the introduction was not supported However the results of the current researches do provide a contribution to the understanding of isolation-induced aggression in young fowl The first study was concerned with the nature of the social stimulation in encounters between chicks and showed that our simplistic notions about the essentials of that stimulation were not warranted The results of the second study drew attention to the motivational consequences of isolation per se and an analysis derived from those results may account for the aggressive consequences of isolation and partial isolation in hatchlings

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studies [Barnett 1963 Reynierse 1971] or may reflect defensive rather th aggressive behavior [Blanchard and Blanchard 1977 Blanchard et al 1977 Moyer 1976] However recently some investigators have reported biting in this situation by rats when they were paired with a guinea pig [Ulrich and A 1962] a mescaline treated rat [Sbordone and Garcia 1977] or a rat with a thesia of the mystacial vibrissae [Ghiselli and Thor 1974] These findings su gest that the victim s behavior in a shock-elicited aggression situation may de mine whether biting occurs In a series of pilot investigations we found that treated rats would often bite rather than box with a Pentobarbital treated op ponent in a shock-elicited aggression situation The present study attempts to systematically investigate the relationship between a Pentobarbital treated ra behavior and the topography of aggressive behavior of an untreated opponen in a shock-elicited aggression situation

## METHODS

### Subjects

Seventy two (72) experimentally naive male Long–Evans rats between 16 180 days old were obtained from the Simonsen Breeding Laboratory Gilroy California Each rat was housed separately with food and water available at all times

### Apparatus

The experimental chamber used in each experiment consisted of a cylindr test chamber with inside dimensions of 30 cm in diameter by 30 cm in heigh The entire chamber was constructed of clear Plexiglas which allowed an u structed view of its interior The grid floor of this chamber consisted of 0 634 cm stainless steel rods spaced 1 27 cm apart (center to center) Electri shock was delivered through the floor grids operating through a Davis Model 255 gr scrambler The duration of shock and the interval between shocks were controlled by two Davis Model D 501 time interval generators The intensity of the shock current was continuously monitored throughout each experime session The behavior of the victim each aggressive episode and the delivery of shock were recorded concurrently on Davis digital counters standard electric cumulative timers and an Esterline Angus 20-channel event reco The latter device provided a permanent paper tape record of the latency of each aggressive episode with respect to shock presentation as well as of its duration and characteristics The test chamber was housed in a sound- a ed room adjacent to the room housing the rest of the apparatus Both obs rvers sat in this adjacent room and observed the test chamber through a glass wi

## Procedure

The subjects were weighed at the beginning of the experiment and were paired together on the basis of similar bodyweight The difference in bodyweight between any pair of rats rarely exceeded 5 gm Each pair of rats was randomly assigned to one of three treatment groups Each treatment group consisted of 12 pairs of rats In the first (Pentobarbital and shock group) one member of each pair was randomly assigned to receive 20 mg of Pentobarbital (Abbot Labs) per kilogram of bodyweight intraperitoneally approximately 5 minutes prior to being placed in the experimental chamber for aggression testing with its untreated opponent Two of the rats however received a supplemental injection of 40% of the initial dosage of the drug immediately prior to being placed in the chamber since they did not appear to be sufficiently anesthetized by the initial dosage In the second (Saline and shock group) one member of each pair was randomly assigned to receive 0 09% of Saline solution per kilogram of body weight intraperitoneally approximately 5 minutes prior to being placed in the experimental chamber with its untreated opponent In the third (Pentobarbital alone) group one member of each pair was randomly assigned to receive 20 mg of Pentobarbital per kilogram of bodyweight intraperitoneally 5 minutes prior to being placed in the experimental chamber with its untreated opponent for 52 5 minutes without shock Two rats in this group received a supplemental injection of 40% of the initial dosage of the drug

With the exception of rats in the Pentobarbital alone group each pair of rats received 100 shocks (2 0 mA 1 5 seconds duration every 30 seconds) One observer continuously recorded the behavior of the drugged rat throughout the experimental session by pressing one of seven microswitches to indicate its behavior according to the following behavioral criteria ataxic head movements (irregular uncoordinated swaying side to side head movements) ataxic trunk and limb movements (irregular uncoordinated postures and gait disturbances that often resulted in a loss of balance and falling to the grid floor) immobile crouch posture (an immobile-crouch posture as described by Grant and MacKintosh 1963) locomotor activity (non ataxic locomotor activity around experimental chamber) upright threat posture (standing on hindfeet and facing opponent) aggressive behavior (striking or biting opponent) no activity (unconscious or fails to engage in any observable behavior) An inter rater reliability coefficient of 0 94 indicated that these behaviors were easily observable and distinguishable from each other

A second observer recorded the aggressive behavior of the untreated rat by pressing one of two microswitches to indicate the type of aggressive attack made upon its drugged opponent The following criteria were used to record the aggressive behavior of the untreated rat boxing (rat strikes another rat

with rapid boxing like movements using its forepaws) biting (rat bites its opponent) An interobserver reliability of 0 99 indicated that these categories were easily observable and distinguishable from each other Both observers were unable to observe each other s recordings and were not permitted to communicate to each other at any time during the experimental session

## RESULTS

While the Pentobarbital treated rats were anesthetized and lay immobile on the grid floor they were never attacked by their untreated opponents even though both received repeated presentations of electric footshock However as effects of the anesthesia began to wear off the drugged animal began to engage in ataxic movements These movements appeared to elicit biting from its untreated opponent However when the animal recovered from the anesthesia and was no longer ataxic it engaged in upright boxing with its untreated opponent when footshock was delivered Figure 1 presents the number of bites that were delivered to drugged rats by their untreated opponents in the three treatment groups It can be seen that untreated rats in the Pentobarbital and shock group delivered a mean of 6 6 bites to their drugged opponent during the experimental session as compared to a mean of 0 7 bites for untreated rats in the Saline and shock group However no aggression was observed when an untreated rat was paired with a drugged opponent in the Pentobarbital alone group None of the drugged rats was ever observed to initiate an aggressive attack on the untreated opponent A one factor ANOVA indicated that the administration of Pentobarbital to one member of the pair of rats exposed to footshock resulted in a significant increase in biting [$F(?,33) =$ 4 58 $P < 0\ 02$] Subsequent Newman–Keuls tests indicated that this group was significantly different from both the Saline and shock ($P < 0\ 05$) and the Pentobarbital alone ($P < 0\ 05$) groups No difference however was found between the Saline and shock and the Pentobarbital alone groups ($P < 0.25$)

Table I presents the relationship between the behavior of the Pentobarbital treated rats prior to attack and the aggressive behavior of their untreated opponents in the Pentobarbital and shock group An analysis of the behavior of the drugged victim immediately prior to an attack by an untreated opponent revealed that 86 1% of the biting attacks occurred after the drugged rat had either engaged in ataxic movements or assumed an immobile crouch posture These behaviors however preceded only 13 1% of the boxing attacks by the untreated rat whereas behaviors such as upright threat postures and locomotor activity occurred immediately prior to 86 9% of the untreated rat s boxing attacks upon the drugged victim these behaviors however preceded only 13 9% of the biting attacks delivered to the drugged rat

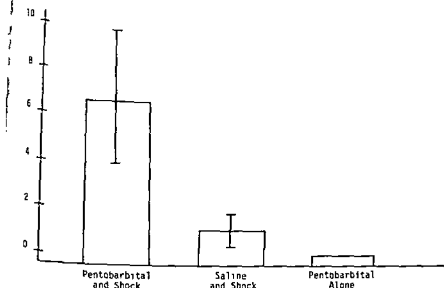



Fig 1 Mean number of bites made by untreated rats for three treatment roups standard error

ABLE I Relationship Between Behavior of Pentobarbital Treated Rat and
e Fighting Behavior of Untreated Opponent in the I entobarbital and Shock Group

| havior of pentobarbital ated rat immediately or to being attacked | Fighting behavior of untreated opponent | | | |
|---|---|---|---|---|
| | Boxing No | ~ | Biting No | ~ |
| ixic head movements | 0 | 0 0 | 42 | 53 ? |
| ixic trunk and limb movements | 8 | 13 1 | 1? | 1 5 |
| mobile-crouch posture | 0 | 0 0 | 9 | 11 4 |
| comotor activity | 16 | ?6 2 | 8 | 10 1 |
| right threat posture | 37 | 60 7 | 8 | 3 8 |
| ressive attack | 0 | 0 0 | 0 | 0 0 |
| activity | 0 | 0 0 | 0 | 0 0 |
| al | 61 | 100 0 | 79 | 100 0 |

An examination of the data revealed that the total amount of time Pentobarbital treated rats engaged in ataxic behaviors and immobile crouch postures during the experimental session was highly correlated with the number of bites they received from their untreated opponents (r = 0 983 df = 11 P < 0 001) Similarly the amount of time these rats engaged in upright threat postures was found to be highly correlated with the number of boxing episodes that occurred during the entire session (r = 0 985 df = 11 P < 0 001)

## DISCUSSION

In the present study Pentobarbital treated rats were never attacked by their untreated opponents when they lay unconscious on the grid floor However as they regained consciousness and began to engage in drug induced ataxic movements they were bitten by their untreated opponents As soon as the ataxic movements disappeared and they were able to assume upright theat postures the biting attacks were replaced by boxing behavior

Two hypotheses may account for this finding The first argues that the drug disrupted ritualistic fighting behavior which is designed to minimize injuries or prevent the occurrence of biting in this situation [Eibl Eibesfeldt 1961] This would account for the occurrence of biting when the drugged animals were unable to assume upright threat postures during the initial part of the experimental session This hypothesis however does not sufficiently explain why the untreated rats in the present study bit their drugged opponents immediately after the latter engaged in ataxic behavior

The second hypothesis argues that the topography of aggressive behavior between a pair of rats in a shock-elicited aggression situation depends on a high degree of standardization in the use of signals which serve functions as preventing attack inducing withdrawal or appeasement Thus the appearance of ataxic behavior might disrupt this communication process or serve to communicate strangeness to the untreated opponent and thus invite aggressive behavior that is usually reserved for strangers or intruders or members of other species This would account for the delivery of biting attacks by untreated rats immediately prior to the ataxic behaviors of the drugged w[illegible] and their disappearance when the ataxic behavior ceased There are studies which support this hypothesis For example when a rat was made ataxic following the administration of mescaline it was bitten by its untreated opp[illegible] when footshock was delivered but engaged in upright boxing when test d[illegible] days later without the drug with the same opponent [Sbordone 1976] when a rat was paired with a guinea pig and both shocked the rat began to bite its head [Ulrich and Azrin 1962]

The data in the present study is consistent with reports of biting by [illegible] rats in a shock-elicited aggression situation [Ghiselli and Thor 1975 Sh[illegible] and Garcia 1977 Ulrich and Azrin 1962] In each of these studies the n[illegible]

spent little time moving around the chamber or in upright postures Similarly Hynan [1976] reported that rats restrained to a supine posture were attacked more frequently by freely moving rats in a shock-elicited aggression situation than when they were restrained to an upright posture Hynan however did not report whether his atattacking rats bit their restrained victims The data in the present study is also consistent with studies which have reported biting by untreated rats in a food competition situation following the administration of Delta 9 Tetrahydrocannabinal [Miczek and Barry 1974] and alcohol [Miczek and Barry 1977] to one member of the pair These investigators reported that these drugs interfered with the animal s ability to assume upright threat postures and prolonged the amount of time spent in immobile-crouch postures None of these studies however attempted to systematically investigate the relationship between the behavior of the victim and the occurrence of boxing or biting behavior by an untreated opponent

The data in the present study suggest that the effectiveness of a particular drug to elicit biting or boxing behavior from untreated rats may be a function of the degree to which that drug influences the behavior of a treated opponent in a situation in which aggressive behavior is likely to occur Since however several investigators have shown that tactile [Ghiselli and Thor 1975 Thor Ghiselli and Lambelet 1974] olfactory [Ghiselli and Thor 1975] and ultrasonic cues [Ghiselli and LaRiviere 1977] may play a major role in the aggressive behavior of rats in a shock-elicited aggression situation it is possible that these cues may accompany the specific behaviors described above Thus further research needs to be done to determine the relative importance of visual tactile olfactory and auditory cues elicited by the victim in determining whether an attacking opponent engages in either biting or boxing behaviors

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AGGRESSIVE BEHAVIOR
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# ;ex Differences in Aggressive Behaviour in Various Strains of Mice

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Two nonalbino inbred (C57 BL/6 and C3H/He) and one albino strain (Swiss) of mice were compared for female aggression toward intruders 1) in period of lactation 2) in nonlactating state and 3) in nonlactating state but previously rubbed with urine of lactating females and for male aggression toward familiar or unfamiliar opponents.

The results showed that resident females of the C57 and Swiss strain vigorously attack lactating intruders introduced into their cages. This effect was mediated by urinary cues emitted by the latter mice It was also shown that Swiss residents displayed aggression towards nonlactating females irrespective of their strain. Groups of C57 residents reacted most aggressively towards Swiss females less aggressively towards C3H intruders but did not show any aggression towards their own nonlactating conspecifics In contrast none of the C3H resident female groups displayed aggression towards intruding females of any category or strain

The results also showed that the males of the three strains displayed l ttle (Swiss and C3H) or no aggression (C57) towards familiar opponents whereas they directed increased aggressive responses towards unfamiliar ones. Comparisons among the three strains of mice revealed that Swiss males were the most aggressive in either situation On the other hand the finding that C3H males showed aggressive responses suggested that male and female aggression are in this strain under separate genetic or hormonal control

y words aggressive behaviour mice d fferent strains lactation maternal urine olfaction

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## INTRODUCTION

In previous studies [Haug 1972 1973] it was shown that urine from nonlactating or lactating females induced aggressive behaviour in small groups of virgin adult females This response was much more frequent against lactating females However this aggressive behaviour was shown to be strain dependent [Haug and Mandel 1978] Thus Swiss mice attacked lactating mice more [illegible] than nonlactating females whereas C3H females did not display aggressive responses against either nonlactating or lactating conspecifics In an inbred strain of mice (C57) attacks occurred only against lactating females

The aim of the following experiments was to test

1) If the urine from C57 or Swiss lactating females can stimulate aggressive responses in their own and in two other strains respectively C3H and Swiss or C57 and C3H 2) if the finding that C3H mice do not react aggressively against lactating females is related to the lack of production of urinary factor 3) if the lack of aggressive behaviour is also specific for males of the C3H strain

## GENERAL METHODS

The three strains of mice used were obtained originally from the C.S.E.A.L.-CNRS Orleans la Source and maintained in our laboratory by inbreeding (C57 C3H) or by outbreeding (Swiss) between different litters The animals were maintained on a 12/12 light/dark cycle with lights on at 8 AM

Two types of experiments were performed In the first 90 groups of three females (residents) of each strain were used At the age of three months each group was tested for aggressive behaviour against intruder females of their own strain or the other two strains of mice that were placed into the home cage (transparent Mackrolon cages 33 × 12 × 18 cm) a) two week lactating females b) [illegible] lactating females c) nonlactating females previously rubbed with urine of lactating females of their own strain

All these categories of intruders were born in our laboratory and were the same age as the resident mice Before the beginning of testing they were kept in colonies of five (nonlactating females) or isolated with their pups (lactating females Ten animals were used for each category of intruders of either strain Urine samples used were collected in metabolism cages which ensure their conservation at very low temperature [see Haug 1976] for rubbing [illegible] intruders

In the second experiment males of the same three strains of mice were used for aggressive encounters On weaning ten groups of five males 30 days old were selected from each strain of mouse and transferred to Makrolon cages in which they had free access to water and food When they were three months old the males were tested for their aggressive behaviour towards other males of the same

train Two types of opponent were u ed namely a) from the same cage (familiar mice) b) from a different cage (unfamiliar mice) In both cases the aggressive respon e measured after putting the randomly selected males in a neutral cage
All experiments were made in a soundproofed enclosure with isotropic light gres ive responses were assessed by monitoring latency time to the first te and the number of bites which occurred during the following 15 (male–male counters) or 30 minutes (female–female encounters) In this last case the umber of bites measured represented the total for the intruder attacking females generally two of the three residents were involved

## SULTS

Table I shows the average number of attacks and the mean attack latency that ident females of the C57 C3H and Swiss strains displayed against strange males of their own and of the two other strains Results obtained with Swiss l C57 residents are also graphically represented (Figs 1–4)
The findings showed that Swiss residents displayed aggression with the same ensity (H = 1 773 df = 2 P > 0 05 Kruskall–Wallis test) and rapidity = 0 780 P > 0 05) against non lactating intruders of their own strain and inst those of the C57 and C3H strains In contrast to Swiss residents groups 57 residents reacted more aggressively to Swiss females than C3H nonlactating ales introduced into their cage (aggression scores differed significantly from se displayed towards C3H females P (attacks) < 0 05 P (latency) < 0 01 deter ed by Mann–Whitney U test) but did not show any aggression against nonlactating ales of their own strain More specifically C3H residents did not display any ession against nonlactating females irrespective of their strain
Other differences were found between these strains of mice when their aggressive onses against lactating intruders were considered Thus the results revealed Swiss residents attack lactating females of their own strain more frequently rapidly than nonlactating ones (P < 0 01) but displayed only a shorter latency n encountering mothers of the C57 (P < 0 01) or C3H (P < 0 01) strains lactating intruder effect was absent from the aggressive behaviour of residents Significantly differences were observed for both criteria between iting and nonlactating intruders from the C57 (P < 0 01) C3H (P < 0 01) and s (P < 0 05) strains In contrast none of the C3H resident female groups nce displayed aggression against intruding mothers of their own or the other ns
he results showed also that rubbing of nonlactating intruders of each strain the corresponding maternal urine increased aggressive responses of C57 and s residents while not affecting the behaviour of C3H residents Generally with s residents the aggressive responses against rubbed females were quite similar o e displayed toward lactating mothers themselves except for intruders of their

**TABLE I** Effect of Strain and Condition of Female Intruders on Their Attack by Resident Females of Three Different Strains

| Resident strain | Aggression measures | C57BL/6 NL | | L | | NL | UL | ML | |
|---|---|---|---|---|---|---|---|---|---|
| C57BL/6 | Mean number of attacks ± SE | 0 | | 16 | 368 | 18 7 | 3 08 | 1 1 | 119 |
| | Mean latency ± SE | >1 800 | | 3 40 | 1650 | 316 | 1658 | 1656 1 | 1441 |
| SWISS ALBINOS | Mean number of attacks ± SE | 10 3 | 1 83 | 18 9 | 3 67 | 4 1 | 1 93 | 11 5 | 1 9 |
| | Mean latency ± SE | 468 1 | 16 5 | 1 90 | 30 5 | 79 0 | 0 0 | 446 0 | 15[illegible] |
| C3H He | Mean latency of attacks ± SE | 0 | | 0 | | 0 | | 0 | |
| | Mean latency ± SE | >1 800[b] | | >1 800 | | >1 800 | | >1 800 | |

[a]Expressed in seconds

[b]No aggression was observed. Intruders were separated from residents after a period of 30 min

own strain which were attacked with shorter latency ($P < 0.01$). In the case of C3H residents however only the rubbed C3H and Swiss intruders were more rapidly attacked ($P < 0.01$ in both cases) when compared to lactating females

The results of the effects of social familiarity or strangeness upon intermale aggression by Swiss C57 and C3H mice are represented in Table II and in the corresponding Figures 5 and 6

Results showed that familiar males of the C3H and Swiss strains attacked each other less often ($P < 0.05$ and $P < 0.01$ respectively) and less rapidly ($P < 0.05$ in both cases) than the unfamiliar mice when they were housed in a [illegible]. Using C57 males aggressive responses were observed only between the [illegible] males of this strain Several other analyses revealed however a strain-dependence of the intensity of aggressive responses between familiar and unfamiliar males. Familiar males of the Swiss strain were as aggressive as unfamiliar males of the C57 and C3H strains (H(attacks) = 0 470 H(latency) = 1 774 for df = 2 $P < 0.05$) [illegible] familiar males of the Swiss strain were much more aggressive than those of the C57 and C3H strains (H(attacks) = 7 932 H(latency) = 7.225 $P < 0.01$) A[illegible] risons between C3H and C57 strains did not reveal significant differences

| C3H/He | | | Swiss Alb nos | |
|---|---|---|---|---|
| L | NL + UL | NL | I | NL UL |
| 15 1 18 | 76 + 18 | 8 9 + 77 | 16 6 ± 1 75 | 4 1 67 |
| 60 4 + 50 5 | 80 4 + 14 8 | 73 4 193 2 | 3 4 6 − 10 1 | 146 3 4 8 |
| 16 1 3 28 | 0 9 + 1 98 | 8 3 – 3 | 3 4 ± 1 66 | 76 ± 1 35 |
| 39 0 ± 30 8 | 10 0 + 3 5 | 6 5 7 00 4 | 113 3 ± 16 0 | 43 0 ± 8 5 |
| 0 | 0 | 0 | 0 | 0 |
| 1 800 | > 1 800 | > 1 800 | > 1 800 | > 1 800 |

## ISCUSSION

The present study has revealed that female residents of Swiss and C57 strains ere generally more aggressive against lactating females than against nonlactating females all strains tested However C3H females showed no aggression towards any type of truder Also odorous factors contained in maternal urine from the three strains mice appear responsible for triggering aggressive responses as shown by the rubbing sts In some cases maternal urine when rubbed on to nonlactating strangers emed to result in more potent stimuli for attack than lactating females themselves owever this tendency was accompanied only by a shorter latency score Such is e case of the behaviour of C57 residents against rubbed C3H and Swiss intruders d of Swiss residents against urine treated animals of their own strain

In order to explain these results several hypotheses might be proposed

### Maternal Urines Do Not Have the Same Capacity for Stimulating Responses

One such hypothesis has already been formulated for mice by Kessler et al [1975] ho observed that inbred males of the DBA strain were more aggressive against

Mean number of attacks

Swiss Intruders | C3H Intruders | C57 Intruders

20

10

NL L NL+UL NL L NL+UL NL L NL+UL

Condition of female intruders

1

RESIDENTS STRAIN SWISS/ALBINOS

Mean latency in second

Swiss Intruders | C3H Intruders | C 57 Intruders

1200

600

NL L NL+UL NL L NL+UL NL L NL+UL

Condition of female intruders

2

RESIDENTS STRAIN : SWISS ALBINOS

Figs 1 and 2 Mean number and latency of attack directed by groups of Swiss [...] residents towards three different types of intruders of their own strain o of the C57 and C3H strains 1) two week lactating females (L) 2) nonlacta[...] females (NL) and 3) nonlactating females rubbed previously with urine of lacta[...]

Mean number of attack

C57 I truders | C3H intruders | Swi Intruders

20

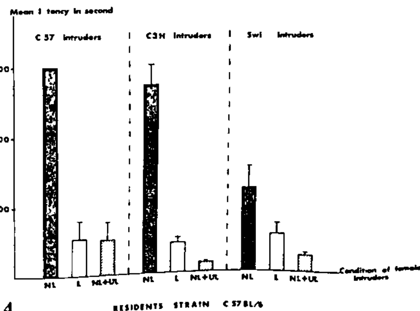
10

NL L NL+UL NL L NL+UL NL L NL+UL

Condition of female intruders

3

RESIDENTS STRAIN C57 BL/6

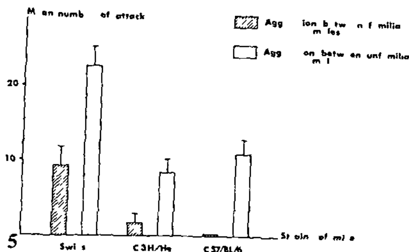


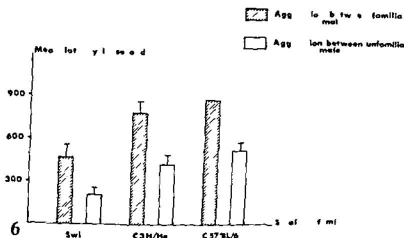

and 4 Mean number and latency of attack directed by groups of C57 female
ts towards three different types of intruders of their own strain or of the
d Swiss strains 1) two-week lactating females (L) ?) nonlactating females
nd 3) nonlactating females rubbed previously with urine of lactating mo

**TABLE II** Fighting in Familiar and Unfamiliar Males of Three Different Strains of Mice in a Novel Arena

| Aggression Measures | C57BL/6 | | C3 /He | | Swiss/Albinos | |
|---|---|---|---|---|---|---|
| | Familiar | Unfamiliar | Familiar | Unfamiliar | Familiar | Unfamiliar |
| Mean number of attacks ± SE | 0 | 11 2 ± 2 03 | 1 9 ± 1 26 | 8 5 ± 1 85 | 9 7 ± 2 62 | 22 9 ± 2 69 |
| Mean latency ± SE | > 900[a] | 542 0 ± 63 5 | 789 0 ± 76 7 | 432 0 ± 72 6 | 474 7 ± 90 4 | 215 0 ± 49 6 |

[a]No aggression was observed Tests are ended after a period of 15 minutes




Figs 5 and 6 Mean number and latency of attack between familiar and unfamiliar adult males from three strains of mice C57 C3H and Swiss

males rubbed with urine of their own strain than against those rubbed with urine from either the CBA or C57Br strains

The absence of aggression observed with C3H females against all intruder mice whether impregnated with urine or not revealed that maternal urine may not constitute an adequate releaser for this type of behaviour (C3H females are in fact capable of presenting another form of aggressive behaviour [Butler 1973] or may exert an inhibitory effect Stimulatory and inhibitory (or aversive) properties of

factors contained in the urines of female [Mugford and Nowell 1970 Dixon a d Mackintosh 1971 Haug, 1972] and male mice [Mackintosh and Grant 1966 and Nowell 1973] have already been demonstrated

**b) The Effects of Maternal Urines Are Potentiated by Other Factors Olfactory or Non-Olfactory Emitted by Intruder Mice**

It is necessary to emphasize that resident females of C57 and Swiss strains attack all lactating mice that produce the urinary factors equally vigorously This suggests that during the period of lactation females can produce one or several factors the effects of which are responsible for the action of urine Frequent biting of glands by resident Swiss mice has been noted [Haug 1972] but the suggestion that milk was involved in this behavior had not been confirmed until recently [Haug 1976]

It is also possible that the degree of familiarity with intruders affects the aggressive responses of females as occurs in male mice The latter possess a nonspecific od which releases aggression as well as a specific odour of identity which sel ctively suppresses the aggression against familiar mice but not against strangers [Rowe et al 1969 Poole and Morgan 1975 Kimelman and Lubow 1974] However the exis of such factors has not been demonstrated in females where this form of aggression has not been studied in detail The present results also reveal that fema of discriminating between two individuals of different strains and that resid attack females of their own strain more rapidly when the latter are rubbed with urine In the same manner residents of the C57 strain attack selectively non- nated mice of the C3H and Swiss strains while not emitting aggressive responses against their own strain [Haug and Mandel 1977]

The role of nonolfactory variables should also be considered Fass and Stevens [1977] have suggested that rubbing adversaries (or intruders) with u es could release visual stimuli involved in aggression However this possibility has been eva- dated by an experiment on genetically blind animals [Lee and Brake 1971] Other factors such as the motility of intruders the rapidity with which they a submissive attitude when attacked the time of appeasement posture th y d [Grant and Mackintosh 1963] and the size of the opponent [White et al 1969] also seem capable of modulating aggression in females

**c) The Three Strains of Mice Do Not Have the Same Olfactory Sensitivity**

Although resident Swiss and C57 mice exhibited different aggressive attit toward lactating and nonlactating mice and though they appeared to discrimina different nonlactating mice placed in their presence one should consider w th strains merely differ in their olfactory sensitivities In fact cases of selec mia having undoubtedly a genetic origin have already been described for th

[Price 1977 Wysocki et al 1977] The absence of aggression of C3H females could be attributed to anosmia On the other hand C3H males (experiment II) are more aggressive against strangers than against cagemates (residents) of the same strain a phenomenon that has been described many times in small rodents [Rowe et al 1969 Poole and Morgan 1975] Little support for the notion that this effect of familiarisati is linked to the perception of olfactory stimuli or if it is (as suggested by Mackintosh and Grant [1966]) that a positive correlation exists between the aggression of males and that of females [Hyde and Ebert 1976 Ebert and Hyde 1976] is evident in the literature so this seems an unlikely possibility

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AGGRESSIVE BEHAVIOR
Volume 4 pages 365–378

# A Guide to the Literature on Aggressive Behavior

Articles relating to the general problem area of aggression are scattered throughout the whole range of specialized journals in fields from A for anatomy to Z for Zoology It is virtually impossible for a single individual to find all the articles which may bear on his particular interest Information overload is of course a problem However an even greater problem is matching the interesting article with the interested reader Aggressive Behavior will attempt to alleviate this problem by publishing a list of references in each issue The reference list will be compiled from several sources Each article listed in Psychological Abstracts and indexed under the following terms will be included

1 Aggressive Behavior
2 Anger
3 Animal Aggressive Behavior
4 Attack Behavior
5 Hostility
6 Threat Postures
7 Violence
8 Frustration
9 Conflict

Each reference will be coded according to the index terms listed above and will be listed in alphabetical order by senior author There are a large number of journals that publish articles related to aggression that are not covered by Psychological Abstracts In order to find such references the cooperation of all readers of this journal is needed If each of the several hundred investigators concerned with the problem of aggression makes a habit of contributing to the literature search section of Aggressive Behavior the search task of each of us will be made easier If in your coverage of the literature you find an article about aggression in a journal that is not regularly abstracted by Psychological *Abstracts put the* full reference on a 3 X 5 card and send it to the editor for inclusion in this section

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